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REVISION

Lichenomphalia umbellifera: fungible and infungible epithets and species concepts

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Supplement to

Voitk, Thorn, & Saar:
Lichenomphalia umbellifera:
fungible and infungible epithets and species concepts
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PROLOGUE

This is a revision of a recently published work (Voitk & al. 2023a). The original publication appeared in what turned out to be the last issue of Mycotaxon, published under trying conditions, following the death of its long-time Editor-in-Chief, Lorelei Norvell (Redhead, Ammirati, Korf & Pennycook 2023). After publication, Scott Redhead notified us that the work contained some nomenclatural errors, the major one being the rejection of a lectotypification for *Agaricus umbellifer* L., which, according to the International Code of Nomenclature for algae, fungi, and plants (Turland & al. 2018; henceforth, the Code), cannot be superseded. This meant that the neotype erected in the original work was not Code compliant. Because Mycotaxon ceased publication after the issue carrying this work, this and a lesser nomenclatural error were corrected in Nomenclatural Novelties of Index Fungorum (Voitk & al. 2023b).

We very much regret these and other errors. The senior author (AV) feels compelled to state that the duties of the authors were divided, and the errors occurred in the segment entrusted to him. Although the errors were technical, in that they did not alter the findings, their interpretation or the conclusions, ideally several sections of the text should be rewritten to reflect the effect of the corrections. In addition to simple substitutions (e.g., replace all 19 instances of "neotype" with "epitype"), more complex discussions needed to be added, like a section examining the fit of *A. umbellifer* with its now retained lectotype (which had been rejected because of a putative conflict with the protologue), as well as dissecting out the relationship of *A. umbellifer* to *A. capillaris* Schumach., which now seem to share the same "original" material.

Detailed review of the work uncovered other areas, where additional change, explanations, emphasis or precision would be an aid to the reader. In addition one discussant revealed a strong preference to conclude either that any name change would be excessively destabilizing, or that Linnaeus, despite what he wrote in the protologue, meant to apply the epithet *umbellifer* to the basidiolichen currently (mis)named *Lichenomphalia umbellifera* (L.) Redhead & al. We did not share these opinions, but because we view past public debates over such differences of opinion somewhat unappealing, we resolved that our task should be complete with laying this information out for the reader. This resolve obliged us to present our interpretations in somewhat greater detail to ensure lucidity. Finally, even the list of nomenclatural novelties, that appears at the end of every volume in Mycotaxon, did not escape fate's mischief: *Lichenomphalia ericetorum* (Pers.) Voitk, Thorn & I. Saar [MB845595], p. 658, appeared erroneously as *Lichenomphalia oniscus* (Fr.) Voitk, Thorn & I. Saar [MB845595], p. 650. It is herewith corrected. When the gods have you in their sights, they do not let you go easily...

After deliberation, we decided that the best service to the reader would be to rewrite the work completely, incorporating all of the above, to present a corrected and more cohesive work. While exploring options where to publish this Review, Noni Korf, manager at Mycotaxon, spontaneously volunteered to host it on the Mycotaxon web site as a Supplement to the original article. We are very grateful to her for arranging this ideal solution at a difficult time, particularly after the issue had already been completed.

REVISION: *Lichenomphalia umbellifera*: fungible and infungible epithets and species concepts

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ABSTRACT

Comparison of the protologue of *Agaricus umbellifer* L. with specimens and descriptions of the basidiolichen *Lichenomphalia umbellifera* (L.) Redhead & al. revealed that the epithet *umbellifera* was grossly misapplied to the basidiolichen, causing several major conflicts with Linnaeus's species concept. In the region where Linnaeus collected *A. umbellifer* we discovered a species of *Marasmius* sect. *Epiphylli*, congruent with Linnaeus's protologue. Because *M.* sect. *Epiphylli* arises from an evolutionary pathway divergent from that leading to *Marasmius* s. str., we erected a new genus, *Owingsia*, to accommodate it, and recombined *A. umbellifer* as *O. umbellifera*, type species of the genus, naming our collection epitype for this species. Molecular studies cemented the concinnity of *A. umbellifer* with our collection: *O. umbellifera* is the most common of several similar species in a complex prevalent in Lapland, where Linnaeus first encountered it, and in the complex, *O. umbellifera* shares the pileal shape of its lectotype and most closely resembles it regarding stipe length, is widely distributed beyond the regions where Linnaeus found it, encompassing the regions of its lecto- and epitype, and sharing substrates with both. The earliest legitimate description of the basidiolichen previously known as *L. umbellifera* is *A. pseudoandrosaceus* Bull., a name superseded by the sanctioned later synonym, *A. ericetorum* Pers. We recombined this basionym as *L. ericetorum*, and epitypified it with a modern sequenced specimen.

Key words *Mycena acicularis*, *Mycena capillaris*, systematics, nomenclature, taxonomy

INTRODUCTION

The basidiolichen currently known as *Lichenomphalia umbellifera* is distributed throughout the Northern Hemisphere (Geml & al. 2012). Because it prefers northern barrens over other habitats, it is ubiquitous in the Canadian province of Newfoundland and Labrador (NL), and the authors know it well: authors AV & RGT have collected it in NL for some 20 years and author IS knows it from her native Estonia. AV can find it regularly about one hour's walk from his front door, on Mt. Ignoble, a hilltop laid barren by forest fire almost 100 years ago. Between 2003 and 2019, Foray Newfoundland & Labrador (FNL, the provincial mushroom club) recorded it 74 times on its annual forays, and AV made 32 collections of it at other times. The basidiolichen has a very variable macroscopic appearance (Fig. 1) regarding colour, shape, and gill arrangement and attachment; basidia with 1, 2, 3, and 4 sterigmata, producing spores smaller in size as the count goes up; diverse habitat tolerance, found from arctoalpine to lowland regions, in barrens, woodlands and even a grassy road embankment; and wide substrate preferences, most prevalent in peat or *Sphagnum* L., but also fruiting on bare ground with moss, on heath, bog, and characteristically on moss-covered fallen logs.

In the early years of surveying the funga of NL, we knew the current *L. umbellifera* as *Omphalina ericetorum*. Three years after its introduction, the newly combined *L. umbellifera* (Redhead & al. 2002) had become the only name used for it on FNL species lists. We applied first one, then the other name, without question. A need to review their protologues and nomenclatural history only arose after almost two decades, precipitated by a taxonomic review of some of its synonyms (Voitk 2022): a preliminary reading of the protologue suggested that the current application of the epithet might be at odds with the original material. This study was undertaken to investigate that question formally. To clearly differentiate between Linnaeus's *Agaricus umbellifer* and the basidiolichen known at the time as *Lichenomphalia umbellifera*, in our discussions we represent the basidiolichen by the contraction Am-min, from "Amanita minima", the first two words of the phrase name informally assigned it by Linnaeus (1732) on his first encounter.

SpeciesFungorum (https://www.speciesfungorum.org/Names/GSDSpecies.asp?RecordID=375200; last accessioned 13 Mar 2022) provides a quick overview of the nomenclatural history of Am-min: a plethora of names have been applied to the species, the earliest binomial being *Agaricus* "*umbelliferus*", introduced by Carl Linnaeus (1753). [In both Classical and Botanical Latin, the correct masculine adjective is *umbellifer*; and the orthographic variant "*umbelliferus*" is correctable according to the Code (Art. 60.1). In total, Am-min has been referred to 19 genera, using 17 different specific epithets, and 21 different subspecific epithets, eight of which have not been used at the species level. These synonyms refer to a wide array of shapes (agaricoid, omphalinoid, umbelliferous, conical), colours (white, yellow, gray, pink, lilac), substrates (algae, turf, leaves, grass,

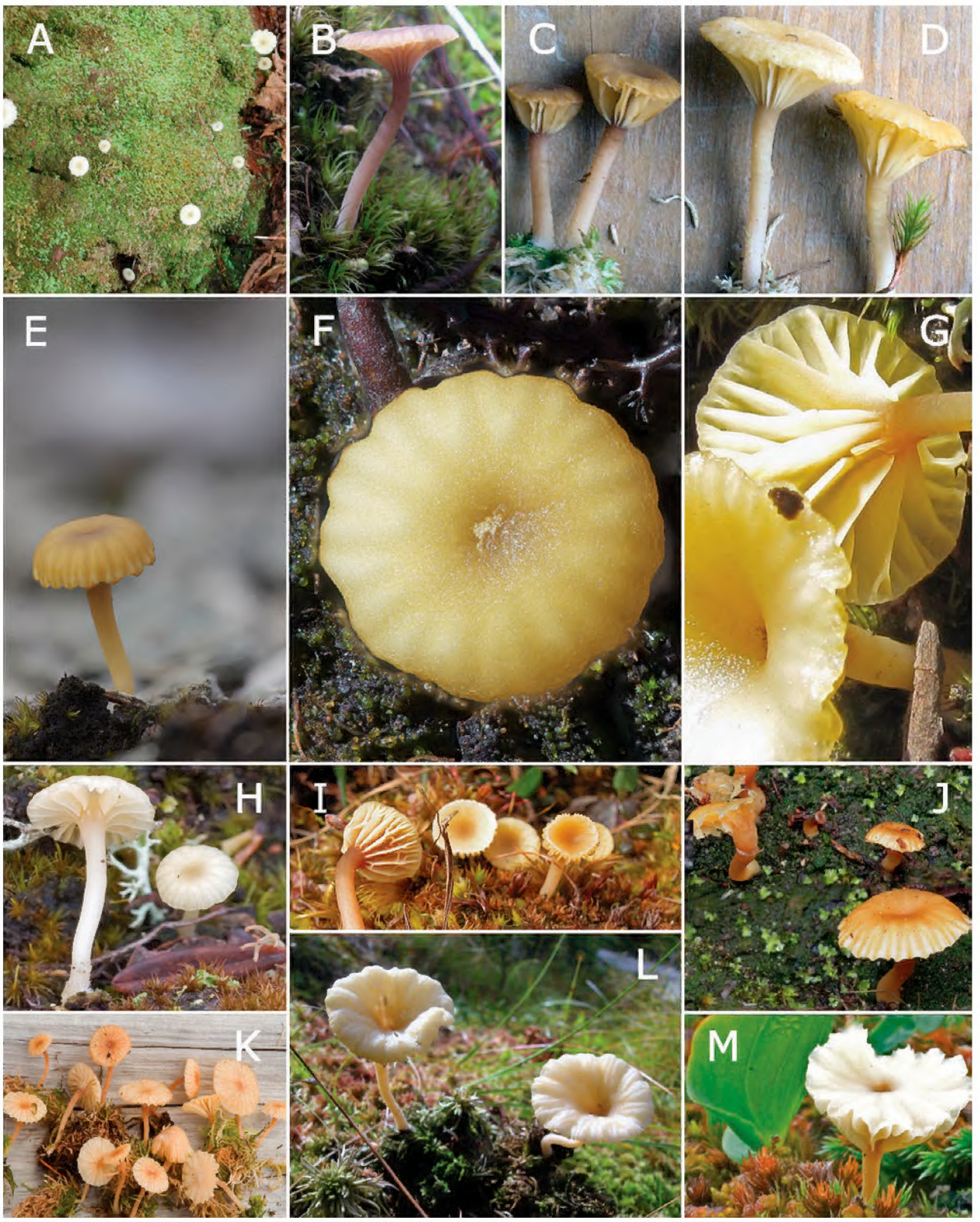

FIG. 1. Collage of several presentations of the mercurial AM-MIN in NL, also showing the fit with many descriptive names used over the years. Colour: from near-white (H, L, M), fitting with "niveus", to yellow (D, F, G), to tan-brown (I, K), to darker or duskier (fuscous) brown (B, C, E, J). At times purplish hues visible, characteristically on the upper stipe (B, C), fitting with "luteolilacina". Pileus near-applanate (K), plano-convex (F, H), convex (E, F), plano-concave (A, B, K), concave (I), deeply infundibuliform (C, D, G, I, L, M); centre depressed (E, F, H, K), umbilicate (B, C, D, I , J, M), deeply umbilicate (G, L), narrow (C, M), or wide (G, I, L). Texture minutely asperous (D, F, G). Lamellae adnate (H, K), arcuate (B, D, G, L), decurrent (D, G, L), segmentiform (C, M, I). Stipe most commonly relatively wide, but on occasion smewhat narrow (A, K, L); less than two cap diameters long, but occasionally close to two cap diameters (I, L); bends upwards on sides of peat pits (A, J), fitting with "turficola"; occasionally with a knock-kneed curve (L), fitting with "valgus". Usually bounteous botryoid lichen thallus readily visible at the base of the stipe (F, J), often covering neighbouring moss or sphagnum (C, D, L).

wood), and other characters, with very little to support a uniform species concept. No doubt the mercurial nature of AM-MIN (FIG. 1) is partly responsible for some of these synonyms, but their profusion and in some cases seeming incompatibility suggests that other factors may be operational as well.

Our plan was to begin by establishing Linnaeus's concept of *Agaricus umbellifer*. Should a clear picture result, it can be tested for fit with AM-MIN. Should it fit, the name is well applied, and our quest is over. Should it not fit, we decided two tasks needed to be completed: 1) identify a fitting species to which *A. umbellifer* can be applied, and 2) find an acceptable name for AM-MIN.

DETERMINING LINNAEUS'S SPECIES CONCEPT OF *AGARICUS UMBELLIFER*

METHOD

All descriptions by Linnaeus (TAB. 1) were examined for uniform and consistent characters, to get an idea of his species concept for this name. The traditional approach of automatically imposing conspecificity on all cited material produced illogical conflicts. This led Redhead & Kuyper (1987) to conclude that Linnaeus (1753) included more than one species when he cited an illustration by Micheli

TABLE 1. Linnaeus's descriptions of AM-MIN & *A. umbellifer*

	Year	Publication	Illustr	name/description	status	quoted	cited
AM-MIN	**1732**	**Iter Lapponica** handwritten journal	AM-MIN, sketch	*Amanita minima infundibuliformis plana, lamellis internis integris, bifurcatis, alternis semi, alba*	phrase name; invalid		
Agaricus umbellifer	**1737**	**Flora Lapponica** published	none	*Agaricus caulescens albus parvus, petiolo longo, pileo plano pellucido, marginae muiltifido*	phrase name; invalid		
	1741	**Iter Œlandicum** handwritten journal	none	*Agaricus minimus capitolo turbinato plano albo, lamellis margine fuscis*	phrase name; invalid		
	1745 a	**Öländska och Gothländska resa** published	none	*Agaricus minimus capitolo turbinato plano albo, lamellis margine fuscis*	phrase name; invalid		
	1745 b	**Flora Suecica 1**	Micheli, Buxbaum	*Agaricus caulescens, pileo plicato membranaceo lamellis basi latioribus*	phrase name; invalid	Fl. Lapp. Öländska, Micheli, Ray	von Haller, Buxbaum
	1753	**Species plantorum 2** **PROTOLOGUE**	Micheli	***Agaricus umbelliferus*** DESCR: Habitat inter folia congesta, semiputrida	binomial; valid	Fl. Suec. 1, Fl. Lapp., Öländska, Micheli	
	1755	**Flora Suecica 2**	Micheli, Buxbaum	*Agaricus umbellifer* DESCR: Habitatat inter semiputrida dejecta folia sylvarum	binomial; valid	Fl. Suec. 1, Fl Lapp., Öländska, Micheli Ray	von Haller Buxbaum

(1729) of a long-stemmed species with a convex pileus, while describing an applanate one. Because claiming that he considered a species with a convex pileus conspecific with one with an applanate one did not make sense (provided he considered cap shape an interspecific character), and because some cited descriptions or illustrations did not seem to agree with others, we agreed with Redhead & Kuyper that Linnaeus likely included more than one species. As a result we decided to avoid assigning an arbitrary synonymy to them that Linnaeus may not have intended. Rather, we assumed that he selected the most accurate match he could find from a limited field of descriptions and illustrations, in order to demonstrate major characters he considered important to *A. umbellifer*, without necessarily considering all conspecific. The concept was developed by ignoring seldom mentioned or unstressed characters, and assigning importance to those characters stressed as important, or common to most descriptions, which supported the description of the protologue (Linnaeus 1753). With this approach, the citations made sense, and enabled us to use cited material with some conflicting elements to note those shared characters specifically stressed by Linnaeus and other cited authors.

For macroscopic description we have tried to follow Vellinga (1988). A few descriptive terms for characters deserve comment. We interpret pellucid, membranaceous, striate and multifid as different ways to indicate a translucent cap with visible radial lamellar projections. We lumped these, along with plicate or a segmented margin, as descriptions of an umbrella-like pileus. Before the days of the turbines and propellers of today, turbinatus was often used to describe a spinning disc of radiating wedges, like the wings of a fan, weathervane, or windmill. We consider turbinatus in that sense: another way to describe an umbrella-like pileus. Funnels were the same then as now, and at the time infundibuliform (funnel-like) was the word indicating a laterally obconical cap. Size is not measured, but generally Linnaeus uses minimus, and certainly parvus for species with a cap diameter around one cm or less. Length is a relative term, in the case of agarics compared to cap diameter. Generally, a stem less than one cap diameter is considered short. A "normal" stem length varies from one to two cap diameters. Usually, the stem must approach or exceed three cap diameters, before "long" is used as a reliable and unmistakable identifying character. In his formal treatments Linnaeus described the gills as broad-based, but did not describe them as decurrent. Cited illustrations did not show gill attachment; we interpret broad-based to have its usual meaning of attached adnate gills. Characters of illustrated treatments are taken from both descriptions and illustrations. A character is considered present in a work only if listed, or quoted in full.

Linnaeus's travels to Lapland were in northern Fennoscandia (not in the modern Finnish political region, Lapland). Throughout this discussion we interpret Lapland as the ethnocultural region Sápmi, traditionally occupied by the Sámi people, encompassing the northern parts of Norway, Sweden and Finland

as well as the adjoining Kola Peninsula of Russia. Because the region has no politically defined borders, its exact extent varies with different descriptions; we used the area defined by Pinto-Guillaume (2017).

Results

Linnaeus's efforts to circumscribe *Agaricus umbellifer* morphologically and ecologically are summarized in Tab. 2. He first described the species in Flora Lapponica (Linnaeus 1737) with the brief phrase name *Agaricus caulescens albus parvus, petiolo longo, pileo plano pellucido, margine multifidio*. In his handwritten journal, Iter Œlandicum (Linnaeus 1741), documenting the Öland leg of his journey to the Swedish islands in the Baltic Sea, he described a species

Table 2. Linnaeus's species concept of *Agaricus umbellifer*, compared to the epitype of *Owingsia umbellifera*

	Basidioma		Pileus			Stipe	Lamellae		Substrate
	white	tiny	flat	plicate	striate	long	distant	broad	leafy
Linnaeus 1737	+	+	+	+	+	+	–	–	–
Linnaeus 1745a	+	+	+	+	–	–	–	–	–
Linnaeus 1745b	+	+	+	+	+	+	+	+	+
Linnaeus 1753 protologue	**+**	**+**	**+**	**+**	**+**	**+**	**+**	**+**	**+**
Linnaeus 1755	+	+	+	+	+	+	+	+	+
Ray 1724	+	+	–	–	–	+	–	–	–
Micheli 1729	+	+	–	–	+	+	+	–	+
Buxbaum 1733	+	+	–	+	–	+	–	–	–
Haller 1742	+	+	+	–	–	+	–	–	+
Total	**9**	**9**	**6**	**6**	**5**	**8**	**4**	**3**	**5**
***Owingsia umbellifera* epitype**	**+**	**+**	**+**	**+**	**+**	**+**	**+**	**+**	**+**

encountered near Kalmar, port of departure for Öland, with the phrase name *Agaricus minimus capitulo turbinato plano albo, lamellis margine fuscis*. The species is redescribed with the same name in the formal published report of that journey, Öländska och Gothländska resa (Linnaeus 1745a). The descriptive phrase names from Lapland and Kalmar differ: the long stipe of the Lapland collection is not mentioned for the Kalmar one, and the former's gill margins were noted to darken. The date of the Lapland find is not given (the journey took place from May 12 to October 10, 1732), but it is significant that the Kalmar specimen was seen May 31. In the first edition of Flora Suecica, Linnaeus (1745b) described species #1033, *Agaricus caulescens, pileo plicato membranaceo lamellis basi latioribus*, quoting both the Lapland and Kalmar phrase names in full, suggesting that he may have considered them the same, despite their differences. The only additional character he noted in 1745 was that the species is epiphyllic, found among decaying fallen leaves (inter semiputrida dejecta folia sylvarum). In addition to his own two phrase names, Linnaeus also quoted phrase names by Micheli (1729) and Ray (1724) in full, cited another by von Haller (1742), as well as illustrations by Micheli and by Buxbaum (1733). Thus, although he did not include long stipe in his own phrase name, he quoted three descriptions in full with this character, and cited another, plus two illustrations

showing a long stipe.

In Species Plantarum (Linnaeus 1753), the work where he introduced use of binomial names, for species # 22, *A. umbellifer*, he quoted in full his phrase names from the Flora Suecica 1, Flora Lapponica, and Öländska och Gothländska resa, (Linnaeus 1745b, 1737, 1745a), as well as the phrase name by Micheli, again citing the latter's illustration. Under the modern Code, the starting date for valid fungal nomenclature has been set back to 1753, making this description the nomenclatural protologue for *A. umbellifer*. As before, the only descriptive information he added was to repeat that the species occurred among piles of decaying leaves. Linnaeus's final treatment of the species came two years later in the second edition of Flora Suecica (Linnaeus 1755) as species #1192. He now used the binomial, quoted his phrase name from the first edition (Linnaeus 1745b), and then repeated the quotations, citations and note about its epiphyllic nature form the first edition.

Despite the somewhat differing Kalmar sighting, the sum of Linnaeus's descriptions and citations gel into a lucid concept, providing solid support to the description in his protologue (Tab. 2): *A. umbellifer* is a small, white mushroom with a flat, somewhat translucent, radially segmented cap, distant adnate gills, a long stem, growing on fallen leaves, widely distributed throughout Europe.

Comments

There is good agreement on stipe length: in addition to the protologue, all Linnaeus's treatments, save the one from Kalmar, either specify a long stem or quote such descriptions in full. All cited authors also describe a long stem. Both cited illustrations (Micheli 1729, reproduced here as Fig. 2A; Buxbaum 1733, reproduced here as Fig. 2B) show a stipe considerably more than three pileus diameters long. Linnaeus repeatedly described the cap as flat. Provided he considered this an interspecific differentiating character, it is unlikely that he selected works or illustrations describing or showing a convex pileus as good examples of conspecificity. Rather, we suspect (but cannot prove) that Linnaeus chose these more to stress the concept of a long stem. This question of pileal curvature, which may have been important for Linnaeus in 1753, and even for Redhead & Kuyper in 1987, is no longer an issue, thanks to technological advances (vide infra).

Likely a second reason for choosing Micheli's illustration was because it clearly illustrated the epiphyllic nature of the species, the same reason Linnaeus cited von Haller (1742), who described a small white mushroom arising **from** (i.e., out of, not between) decomposing beech leaves (**ex** folio fagino putrido). Linnaeus's "inter folia" has been interpreted to mean among (in the sense of between) leaves rather than on them (Jørgensen & Ryman 1994), a somewhat uncomfortable point of view. First, Jørgensen & Ryman themselves state that Linnaeus's attention to ecological detail was lax. Hence, the difference between "among", "on", and "from" may be part of this laxity, in which case assigning

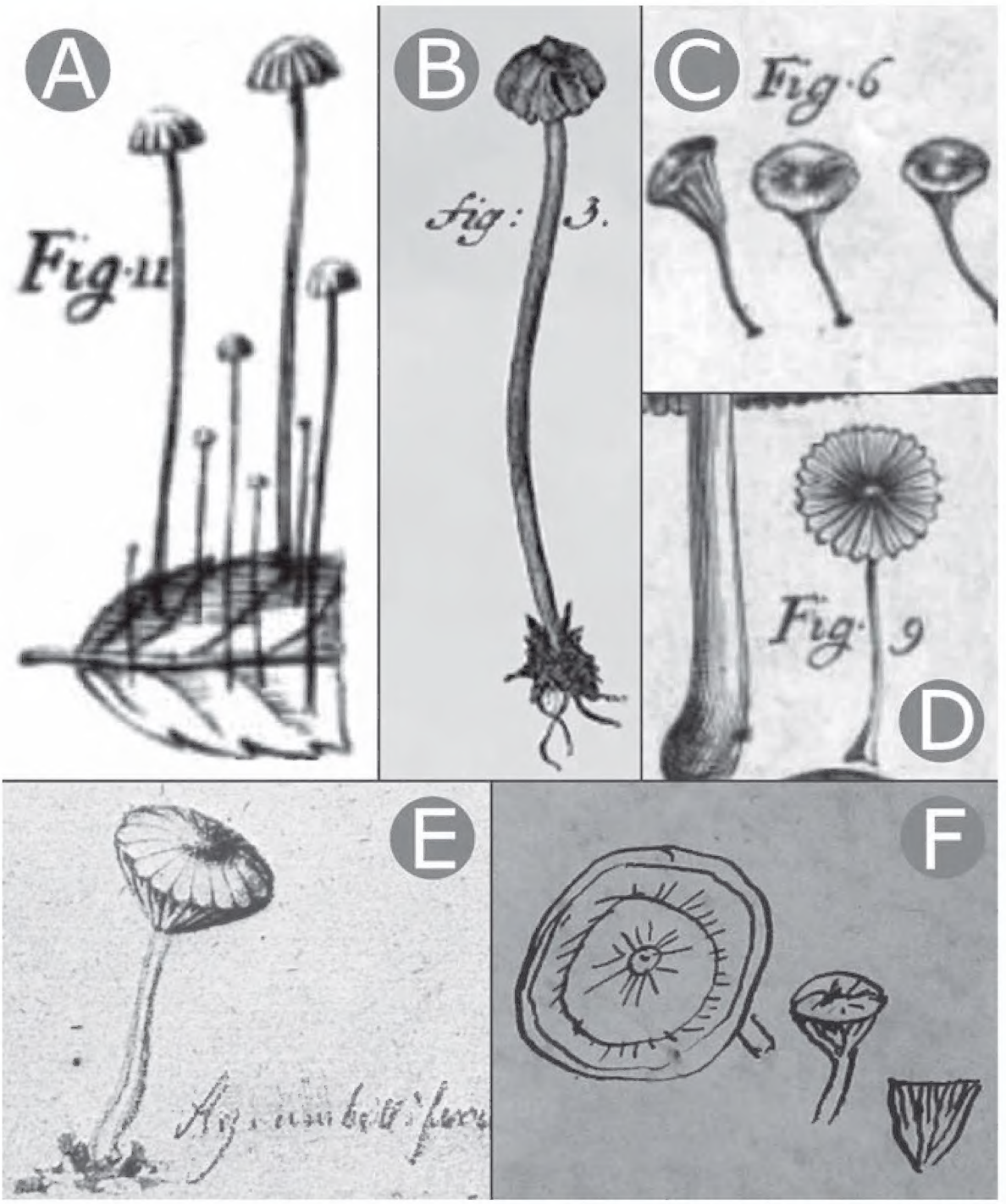

Fig. 2. Past images related or unrelated to *Agaricus umbellifer*: A. Illustration by Micheli (1729) cited by Linnaeus (1745b, 1753, 1755); no doubt about the long stem and epiphyllic nature of the species; B. Illustration by Buxbaum (1733), cited by Linnaeus (1745b, 1753, 1755), illustrating Linnaeus's concept of a long stem; C. Illustration by Micheli (1729) available to but not cited by Linnaeus, of a species much closer to Am-min than the image he selected; D. Illustration by Micheli (1729) available to but not cited by Linnaeus, of a species somewhat closer to Am-min than the image he selected; selecting the image shown in A, not the ones in C & D, shows that Linnaeus did not have an Am-min-like species in mind for his epithet *umbellifer*; E. Rudbeck's unlabelled illustration from his tour of Lapland, believed to represent Am-min; F. Linnaeus's sketch from his log of his tour of Lapland, which he described with a phrase name, also believed to represent Am-min; note the similarity of E & F (and their similarity to C & D, but significant difference from A & B); clearly both Linnaeus and his mentor Rudbeck were familiar with Am-min; neither E nor F was cited in the description of *A. umbellifer*, again demonstrating that Am-min was not Linnaeus's species concept of *A. umbellifer*.

literal interpretation may lead to error. Secondly, it is clear that, lax or not, the association with leaves was significant to Linnaeus, because he repeated this character in all three formal treatments (Linnaeus 1745b, 1753, 1755) giving it extra stress by inserting it separately at the end of each description, the only character that he felt important enough to add separately to the phrase names. Thirdly, in the protologue Linnaeus (1753) specified growth on PILED decomposing leaves (folia CONGESTA, semiputrida), a situation where growing ON, rather than between leaves seems unavoidable. Finally, citing von Haller's description of an epiphyllic species twice and Micheli's similar illustration three times cannot be dismissed as random.

TESTING THE FIT OF LINNAEUS'S CONCEPT WITH AM-MIN

TABLE 3 compares Linnaeus's species concept of *A. umbellifer*, as developed above, with AM-MIN. They differ in shape, size, and colour, and have conflicting differences in stem length (relative to cap diameter) and substrate preference. While some of the differences in characters have been the subject of past debate, this analysis leaves little doubt about their validity. The number of irreconcilable

TABLE 3. Comparison of Linnaeus's species concept of Agaricus umbellifer and AM-MIN

	Basic color	Cap diameter	Cap shape, commonest mature	Stem length	Gill spacing	Substrate, preferred
Owingsia umbellifera	White	≤1 cm	planoconvex to applanate	≥3× cap diam.	distant/reduced	dead leaves
AM-MIN	Yellowish	>1 cm	Funnel	≤1.5× cap diam.	moderate	turf

major characters between *A. umbellifer* and AM-MIN makes it clear that Linnaeus had a species other than AM-MIN in mind for *A. umbellifer*. The above is not a new discovery or an original conclusion. Redhead & Weresub (1978) documented it, and Redhead & Kuyper (1987), looking at the same information discussed here, came to the same conclusion. Further, they demonstrated that had Linnaeus wished to apply *A. umbellifer* to AM-MIN, he had images of species with an omphalinoid pileus and shorter stipe (two reproduced here as FIGS 2C & 2D) available to him among Micheli's illustrations (Micheli 1729), that were far more AM-MIN-like than the one he chose (reproduced here as FIG. 2A).

Surely the most compelling evidence, not discussed earlier, that Linnaeus did not consider *A. umbellifer* to be AM-MIN, is that both Linnaeus and his mentor, Olof Rudbeck, KNEW AM-MIN. Both had undertaken Lapland journeys, where both had seen this iconic species of northern heaths, and both had made readily identifiable illustrations of it. Rudbeck's 1695 journal, Iter Lapponicum—skissboken från resan till Lappland, was published posthumously (Anfält 1987). There is no evidence that Rudbeck described or named the species, but he left an illustration (reproduced here as FIG. 2E). Linnaeus's journal, handwritten in Swedish and also entitled Iter Lapponicum (Linnaeus 1732), became generally available in

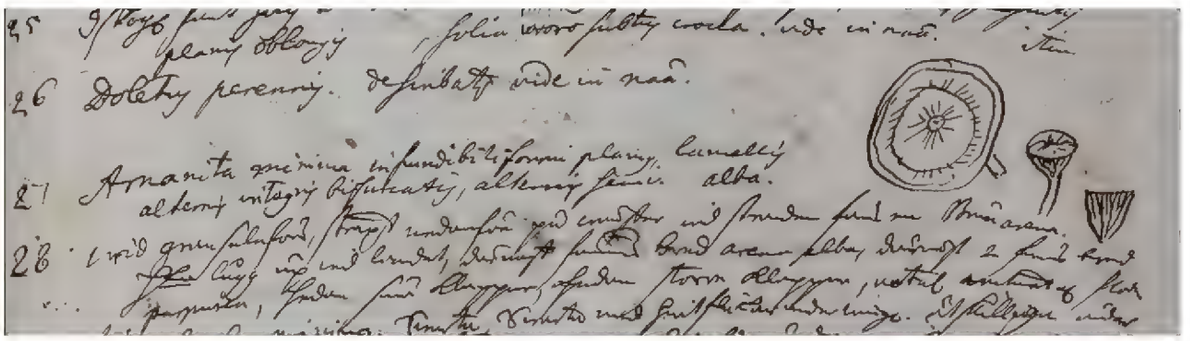

FIG. 3. Part of Linnaeus's journal, Iter Lapponicum, with his handwritten phrase name and famous sketch of AM-MIN, the source of FIG. 2 F.

1811, when Sir James Edward Smith edited an initial translation by Charles Troilius, and published it in two volumes (Smith 1811). Sir James bought Iter Lapponicum as part of the Linnaeus collection from Linnaeus's son, and founded the Linnaean Society of London, which became the custodian of Linnaeus's papers. T.M. Fries (1913) also helped make Linnaeus's Iter Lapponicum much more available to scholars through a posthumous publication of an annotated typed transcription of Linnaeus's journal in the original Swedish. In this journal Linnaeus gave item 27, noted on May 31, the descriptive phrase name, *Amanita minima, infundibuliformi plana, lamellis alternis integris, bifurcates, alternis semi, alba*—the source (as mentioned) for our contraction AM-MIN—and made an illustration immediately recognizable as AM-MIN (reproduced here as FIG. 3). Note that Linnaeus applied *Amanita* quite differently from its current usage. The name was introduced by Dillenius (1719) for one of four genera of fungi, the genus with pileus, stipe, and lamellae—in other words the group we now refer to as agarics. Linnaeus admired Dillenius, visited him in Oxford in 1736, and initially followed his classification.

With the help of T. M. Fries's second Swedish edition to overcome difficulties reading 18th century Swedish in Linnaeus's handwriting, augmented by Sir James's English translation, we examined whether the AM-MIN Linnaeus's treated in his journal could be the same species he introduced in the formal Flora Lapponica. The evidence does not support such speculation: Flora Lapponica presented an entirely different species. At the time phrase names, although descriptive, were treated as names, quoted in full. For example, when Linnaeus treated the immediately preceding taxon, *Boletus perennis*, in Flora Lapponica, he used the same phrase name as he used in the journal. Similarly, when he redescribed *Agaricus minimus capitulo turbinato plano albo, lamellis margine fusci* from his journal of the expedition to Öland, Iter Œlandicum, he used the same name, *Agaricus minimus capitulo turbinato plano albo, lamellis margine fusci*, when treating it in the formal published report of that journey, Öländska och Gothländska resa. On the other hand, the name he used for AM-MIN in Iter Lapponicum, his handwritten journal of the Lapland journey, was *Amanita minima, infundibuliformis plana, lamellis alternis integris, bifurcates, alternis semi, alba*, not the name of the different species he reported formally

in Flora Lapponica: *Agaricus caulescens albus parvus, petiolo longo, pileo plano pellucido, margine multifidio*. When he translated Linnaeus's journal, Sir James noted taxa also treated in the formal Flora Lapponica. Thus, for item 26, immediately above, *Boletus perennis*, Sir James adds that it was treated in the Flora, and as is the custom, under the same name. No such annotation is made for the next item, number 27, Am-min, under any name. Not only do the two names differ, but the descriptions also differ significantly from each other. Am-min, is small (minima), *A. umbellifer* is lesser (parvus); Am-min is funnel-shaped (infundibuliformis), a term he never applied to *A. umbellifer*, with a flat top (plana), *A. umbellifer* has a flat translucent top (plano pellucido), translucence being more obvious with a thin cap, rather than a funnel-shaped structure; the gills of Am-min bifurcate, seen regularly with that species, but not with *A. umbellifer* with its reduced gills; most importantly, no mention of a long stem is made when describing Am-min, whereas this signature character (petiole longo) is described for *A. umbellifer*.

The Code directs us to follow the protologue and its original material. Linnaeus never quoted the name with which he introduced Am-min again, never cited it, and never treated it with a valid binomial. As clearly demonstrated by Redhead & Weresub (1978) and explained by Redhead & Kuyper (1987), applying *A. umbellifer* to Am-min is incompatible with the protologue and its original material.

Why, then, did this epithet still get applied to Am-min? Two years after Redhead & Kuyper's conclusion, where they typified *A. umbellifer* with the illustration by Micheli cited by Linnaeus, Jørgensen & Ryman (1989) proposed Rudbeck's aquarelle of Am-min (reproduced here as Fig. 2E), as lectotype for *A. umbellifer*, stating, "Judging from the **descriptions** and the **circumstances** (cf. Linnaeus 1737: 352, point 1) it is likely that Linnaeus based the description entirely on this drawing." Coming to this debate over 30 years later, without prejudice for either side (until we began this enquiry, we had accepted *Lichenomphalia umbellifera* as the appropriate name for Am-min, and had not been aware of this controversy), we developed Linnaeus's species concept from his writings (Tab. 2), and compared that with Am-min (Tab. 3), which led us to conclude that Linnaeus's description of *A. umbellifer* does **NOT** fit Am-min. Consequently, we cannot agree with Jørgensen & Ryman (1989) that Linnaeus's **descriptions** suggest this drawing was used to create the protologue. The **circumstances** Jørgensen & Ryman (1989) refer to, citing Linnaeus's introduction to the section dealing with *Fungi* in his Flora Lapponica, consist of references by Linnaeus to a fire that destroyed many books and good source material, and grateful expressions of relief that many of Rudbeck's illustrations had been kept safe from fire. Linnaeus thanks Rudbeck for putting these ("eos", note the plural) at his disposal. Thus, certainly Linnaeus acknowledges the availability of Rudbeck's material for his book, but speaks of illustrations in the plural (as do Jørgensen & Ryman), and nowhere does Linnaeus mention that any particular illustration was used for

the description of any particular species. There is no record from Linnaeus or others that Rudbeck's unnamed and unpublished drawing of an undescribed species—or any particular illustration—was the basis for species #471 in his Flora Lapponica, or elsewhere. There is a vast gap between having **SEVERAL** illustrations at one's disposal, and using one specific illustration to describe one specific species. Nothing in Jørgensen & Ryman's subsequent two paragraphs support their changing the probable "it is likely" in the above quote to the certain, "we have also **PROVED**" that Linnaeus had AM-MIN in mind when describing *A. umbellifer*—in fact, quite the opposite—and we find nothing to support referring to Rudbeck's drawing as "original material" for *A. umbellifer*.

We do not claim that Linnaeus did not have access to Rudbeck's Lapland material, including the drawing under question. The logical assumption would be entirely opposite. Olof Rudbeck fil. (1660–1740) was a Swedish scientist and explorer, who joined an expedition to Lapland commissioned by the King of Sweden. At that time Lapland still had the draw of terra incognita, even in Scandinavia. Unfortunately, most of Rudbeck's collections and many records from that journey were lost in a fire, but some paintings and his journal-sketchbook survived to be published posthumously. Rudbeck was mentor to the young Linnaeus, when the latter began his pursuit of botany and medicine. It is easy to imagine that the exciting tales of the mentor, supplemented by notes and illustrations, kindled enthusiasm for Lapland in his young student. Our guess is that Rudbeck made the material available to Linnaeus already before the latter's own Lapland journey; possibly these helped spur the 25-year-old Linnaeus to undertake a Lapland journey of his own. It is equally reasonable to assume that his mentor continued to share his tales, notes, and records of the earlier journey with his protégé after the latter's return, earning him the thanks noted by Jørgensen & Ryman. Also, there is no reason to doubt that the unpublished material that Rudbeck put at Linnaeus's disposal contained the lovely illustration of AM-MIN. The description of species #471, however, especially of its long stem and its leafy substrate, does not fit Rudbeck's illustration (stem measured just under 1.5× cap diameter, substrate seeming to be mossy soil), making it extremely difficult to accept that one was based on the other.

While we find no similarity between Linnaeus's description of *A. umbellifer* and Rudbeck's illustration, we note the uncanny similarity of Rudbeck's illustration (reproduced here as FIG. 2E) to Linnaeus's sketch of AM-MIN (reproduced here as FIG. 3) in the journal of his own Lapland journey. Linnaeus's described AM-MIN as infundibuliform, which fits both his and Rudbeck's sketches, but neither he nor authors he cited ever used that term to describe *A. umbellifer*. Linnaeus made no suggestion then or later that this sketch represents his concept of *A. umbellifer*. The two journals offer clear proof that both Rudbeck and Linnaeus **KNEW** AM-MIN, but that it was not the species to which Linnaeus applied the binomial *Agaricus umbellifer*. Such suggestions were made later by others. In the case of Rudbeck's illustration, somebody other than Rudbeck wrote,

"*A. umbelliferus* L. Fl. Su. v II 1192" on the illustration, referring to *Agaricus umbellifer*, species #1192, p. 440, in Linnaeus's Flora Suecica vol. 2 (Linnaeus 1755). Jørgensen & Ryman (1989) quoted Nilsson's opinion (Nilsson 1987) that this was added by the botanist Carl Johan Hartman, either 1811–1814 or 1841. Our guess is that this was not a novel idea by Hartman, but that he was influenced in this by a common misunderstanding that Fries (1821) synonymized *Agaricus ericetorum* Pers. with *A. umbellifer* L. (vide infra). If that is so, and if those are the only possible dates of the annotation, then the likely year was 1841. In the case of Linnaeus's sketch in his Iter Lapponicum, the species is identified as "*Agaricus (Omphalia) umbellifer* Fr." not by Linnaeus, but by T.M. Fries on the reproduction (reproduced here as Fig. 2F) in his 1913 Swedish publication of Linnaeus's journal. Parenthetically, it is worth noting that there is no valid taxon, "*A. umbellifer* Fr." Fries treated the species twice (Fries 1825, 1828), and both times specified clearly that he was referring to the taxon of Linnaeus.

Both Redhead and Kuyper remained silent, effectively ending the debate. It took over a decade before Redhead, with different collaborators (Redhead & al. 2002), published a major revision of omphalinoid genera, which required, inter alia, nomenclaturally suitable type species to be assigned to *Arrhenia* and *Omphalina*, while transferring Am-min to their newly erected genus, *Lichenomphalia*, created for lichenized omphalinoid basidiomycetes. This was accomplished by synonymizing and otherwise resolving various competing names and interpretations for *A. umbellifer* and *A. ericetorum*. To do this, they took advantage of a recent change to the International Code of Botanical Nomenclature (Greuter & al. 2000), which now permitted acceptance of the lectotype declared by Jørgensen & Ryman, namely Rudbeck's illustration. Redhead & al. rejected Redhead & Kuyper's earlier typification of *A. umbellifer*, and accepted Jørgensen & Ryman's instead, thereby applying the epithet coined by Linnaeus to Am-min. This contrivance avoided further debate in solving the systematics of the genera of their interest—including getting smooth acceptance of their new genus *Lichenomphalia*—at the expense of ignoring interspecific characters of morphological diversity. Neither Redhead & Kuyper, jointly or separately, nor Redhead and his new collaborators, ever—ever—mentioned, challenged, rebutted, refuted, or withdrew Redhead & Kuyper's published observations regarding the obvious misapplication of *umbellifer* to Am-min. Further, Redhead & al. (2002) did not embrace Jørgensen & Ryman's claim that the Rudbeck sketch was the only image on which Linnaeus based his description of *A. umbellifer*. Rather, they noted the sketch had been "**apparently** available to Linnaeus." This statement certainly did not support the claim that the illustration was part of the original material, and Redhead & al. (2002) offered no discussion whether such **apparent** availability equated to being even a partial source, let alone the **sole** source for Linnaeus's conflicting description. Further, they did not claim that the protologue for *A. umbellifer* was even remotely congruent with Am-min, but rather referred to its application as a "**compromise**", one they

hoped would "resolve and end a 250-year old controversy over these names."

Acceptance of that lecto-typification by Redhead & al. (2002) did not alter its legitimacy, and the problems created by accepting *A. umbellifer* as the basionym of Am-min remained exactly as Redhead & Kuyper (1987) had outlined them earlier (confirmed here): the epithet remained misapplied to Am-min. All available evidence still suggested that Rudbeck's illustration was not the original material for the protologue of *A. umbellifer*, and Linnaeus did not use it as a basis for his protologue—a matter, as pointed out, that Redhead & al. (2002) were careful to skirt. We reject this lectotype by Jørgensen & Ryman because there is no evidence it was used as original material by Linnaeus, and it is in major conflict with the Linnaean protologue. This rejection automatically rejects the subsequent adoption of Rudbeck's illustration as lectotype by Redhead & al.

While emending *Omphalina* Quél., Morten Lange (1981), in the belief that *A. ericetorum* and *A. umbellifer* were synonymous, neotypified *O. umbellifera* (i.e., the basionym, *A. umbelliferus* L.) with specimen 1753 from Fungi Exsiccati Suecici (UPS), shown since to be Am-min (Redhead & al. 2002). Jørgensen & Ryman (1994), also believing in the synonymy of *A. umbellifer* and *A. ericetorum*, declared the same specimen 1753 from Fungi Exsiccati Suecici (UPS), epitype for both taxa. Because we present evidence here that the names *A. umbellifer* and *A. ericetorum* represent two different species, both M. Lange's and Jørgensen & Ryman's typifications are rejected as without standing according to the Code (Arts 9.18 and 9.20). This leaves Micheli's drawing, Tab. 80, Fig. 11, cited by Linnaeus in the protologue, and declared lectotype for *A. umbellifer* by Redhead & Kuyper in 1987. The current Code does not permit superseding this lectotypification (Art. F.3.9 and its Note 2 [May & al. 2019] and Art. 9.19, Note 7 [Turland & al. 2018]).

SEARCH FOR A SPECIES TO FIT LINNAEUS'S CONCEPT OF *AGARICUS UMBELLIFER*

Background

On a trip to Lapland in 2006, the senior author collected a small white epiphyllic agaric with a membranaceous, translucent, flat, umbrella-like segmented cap, and distant gills, supported by a long white stem, arising from that year's fallen leaves of *Populus tremula* L. (Fig. 4). He identified the collection tentatively as *Marasmius tremulae* Velen., and placed it in his personal herbarium. There it remained as collection 06.10.04.av01, altogether forgotten until this study gave rise to a lucid picture of Linnaeus's species concept of *A. umbellifer*. Immediately, this collection came to mind. On review, the collection shared all the criteria of Linnaeus's *A. umbellifer* (Tab. 2, bottom row), including the shape of the cap, which had been a problem in the past. To learn whether this species, fitting Linnaeus's description, could be the species Linnaeus described, we undertook to determine whether the species is prevalent in the regions explored by Linnaeus; in other words, is it likely that Linnaeus would have encountered this same species?

FIG. 4. *Owingsia umbellifera* (A–D = epitype, O-F-76596; E–I = TUF118289): A: Basidiomata on fallen leaves of *Populus tremula*. Note the white, flat, pellucid, umbrella-like caps, long stem, equal or longer than three cap diameters, widely spaced gills, broader at their base, and the many white rhizomorphs/sterile stipes. B: Epitype collection exsiccatum. C: Basidia, mostly four-spored, with about 15% 2-spored (not due to focal length artefact). D: Cystidia. E: Cheilocystidia. F: Pleurocystidia. G: Caulocystidia. H: Pileocystidia. I: Pileipellis elements. Scale bars: A, B = 5 mm; C, D = 5 µm; E–I = 25 µm.

Fig. 5. Map of Fennoscandia and environs, showing the origin of sequenced specimens of *Owingsia umbellifera* (yellow circles; star for epitype) from the two sites where Linnaeus collected them, Lapland (green hatching) and Öland (Ö). Specimens from Öland did not yield DNA, but specimens from nearby Saaremaa (S), and the west coast of continental Estonia, both in/on the Baltic Sea, are shown instead.

Method

Collections identified as *M. tremulae* or *M. epiphyllus* (Pers.) Fr. from around the two places Linnaeus sighted species he referred to *A. umbellifer*, Lapland and Kalmar (Fig. 5), were sought for molecular studies, augmented by additional specimens or sequences from a wider range. Related sequences from GenBank and UNITE (Kõljalg & al. 2013, Nilsson & al. 2019) were added to the analysis (Tab. 4) to construct a phylogeny (Fig. 6) which reflected an approximation of its global distribution. ITS-DNA processing followed Voitk & al. (2020) and phylogenetic analysis Voitk & al. (2022). New sequences were deposited in UNITE and/or GenBank. Where available, note was made of the substrate. Specimens were vouchered in the Herbarium, University of Oslo, Norway (O), the Fungarium, University of Tartu, Estonia (TUF), and the Herbarium, University of Western Ontario, London, Canada (UWO).

Results

Bayesian analysis (Ronquist & al. 2012) showed that *Marasmiaceae*, containing the genus *Marasmius*, formed a sister clade to *Physalacriaceae*, where our specimen fell, with 29 other sequenced specimens, which split among four species (Fig. 6, 7). Maximum likelihood analysis (Stamatakis 2014) of the same material placed the last two Bayesian clades into a single one with 84% support. The genus where these sequences clustered is undescribed, but other studies have shown they belong to *Marasmius* sect. *Epiphylli* Kühner (Owings 1997, Owings & Desjardin 1997, Wilson & Desjardin 2005, Jenkinson & al. 2014). Originally 27 of the studied 30 collections had been identified as *M. epiphyllus* and none other than ours was first identified as *M. tremulae*. Our collection from the Norwegian part of Lapland fell into the largest species clade with 21

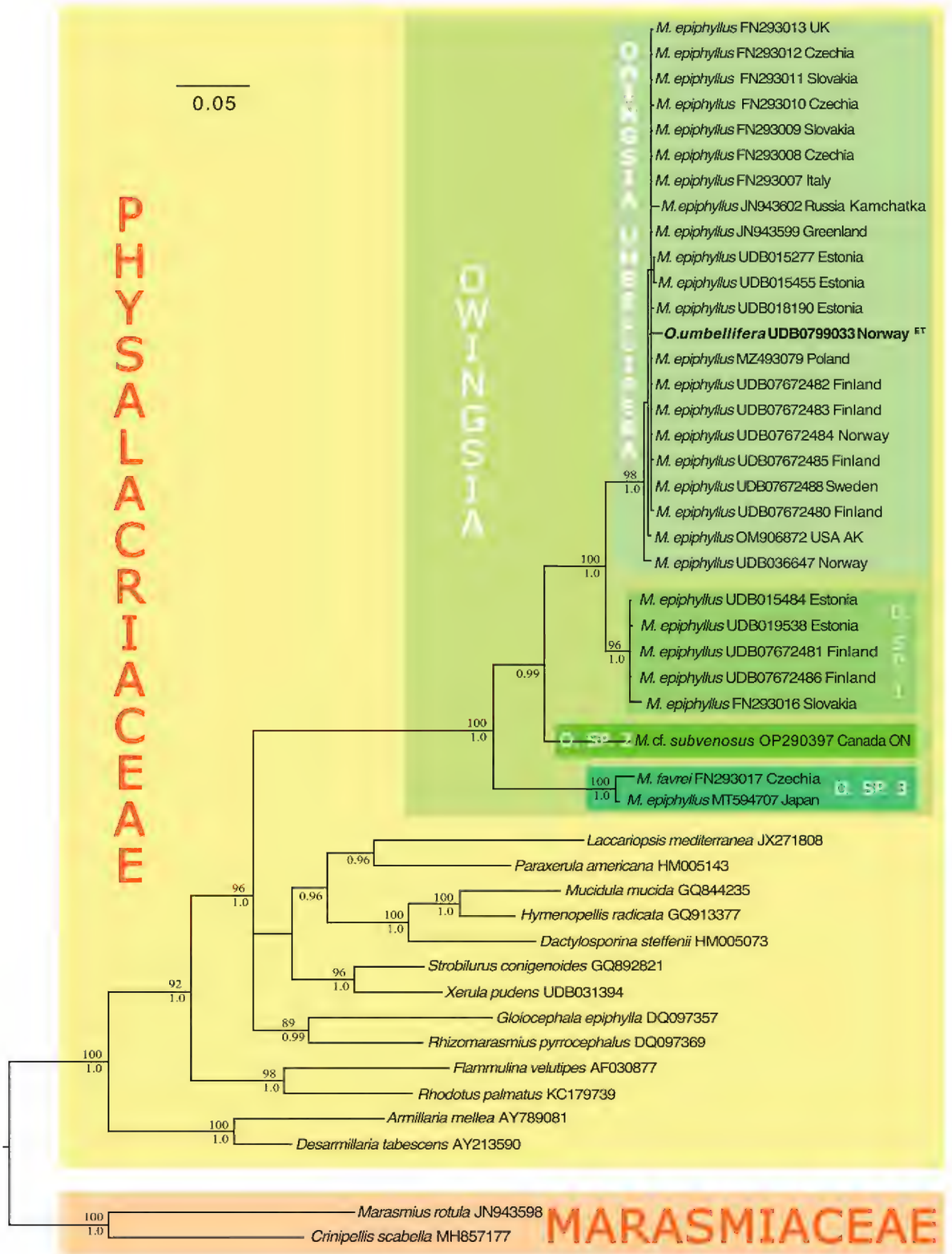

FIG. 6. ITS-based phylogenetic pathways, showing the placement of *Owingsia* in Physalacriaceae, here sister to Marasmiaceae, containing *Marasmius* s.str. Bayesian analysis shows that the genus contains *O. umbellifera* and three other clades of unidentified species to which the name *M. epiphyllus* has been applied. ML bootstrap support ≥70% and the Bayesian posterior probabilities ≥95% are shown above and below the branches (bs/pp), respectively. Maximal likelihood analysis placed *Owingsia* spp. 2 and 3 in a single clade with 84% support. Sequences are identified by the name recorded in the genetic depository or fungarium accession database, with the exception of the epitype, identified by its current name. This limited sampling is inadequate to resolve the genus, a question beyond the scope of this work. *Owingsia umbellifera* is widely distributed, documented in North America from Alaska and Greenland, and in Eurasia from Scandinavia to Kamchatka. The epitype from the Norwegian part of Lapland appears in bold print. The two sister species, *O. umbellifera* and *Owingsia* spp 1, were sympatric, and several recorded on the same substrate, dead leaves of *Populus tremula*.

Table 4. Collections and sequences used in phylogenetic analyses.
Epitype in bold print.

Species	Country	Fungarium no. (duplicate no.)	ITS	Publication
Owingsia umbellifera	Czechia	BRNM695733	FN293008	Antonín & al. 2010
	Czechia	PRM902346	FN293010	Antonín & al. 2010
	Czechia	PRM894159	FN293012	Antonín & al. 2010
	Estonia	TUF106979	UDB015277	UNITE
	Estonia	TUF118289	UDB015455	UNITE
	Estonia	TUF118453	UDB018190	UNITE
	Finland	OULU-F-16597	UDB07672480	This study
	Finland	OULU-F-16603	UDB07672482	This study
	Finland	OULU-F-16606	UDB07672483	This study
	Finland	OULU-F-24076	UDB07672485	This study
	Greenland	NN048205[a]	JN943599	Schoch & al. 2012
	Italy	BRNM695779	FN293007	Antonín & al. 2010
	Norway	OULU-F-21543	UDB07672484	This study
	Norway	**O-F-76596 TUF117828**	**UDB0799033**	**This study**
	Norway	O-F-21830	UDB036647 NOBAS2883-16	UNITE
	Poland	FeF427	MZ493079	Bilanski & Kowalski, unpubl.
	Russia	NN050222[a]	JN943602	Schoch & al. 2012
	Slovakia	PRM870457	FN293009	Antonín & al. 2010
	Slovakia	BRNM523367	FN293011	Antonín & al. 2010
	Sweden	UPS-F-740369	UDB07672488	This study
	UK	K(M)40466	FN293013	Antonín & al. 2010
	USA	MF80535 NS3148	OM906872	Mohatt & al., direct sub.
Owingsia sp. 1	Estonia	TUF118324	UDB015484	UNITE
	Estonia	TUF118729	UDB019538	UNITE
	Finland	OULU10007053	UDB07672481	This study
	Finland	OULU-F-24077	UDB07672486	This study
	Slovakia	BRNM523372	FN293016	Antonín & al. 2010
Owingsia sp. 2	Canada	UWO-F3413	OP290397	This study
Owingsia sp. 3	Czechia	BRNM695419	FN293017	Antonín & al. 2010
	Japan	soil sequence	MT594707	Favero Longo & al., unpub.
Other Physalacriaceae				
Armillaria mellea	—	PBM2470 AFTOL-449	AY789081	Binder & al. 2006
Dactylosporina steffenii	Costa Rica	TENN58785	HM005073	Petersen & Hughes 2010
Desarmillaria tabescens	USA	00i-99	AY213590	Kim & al. 2006
Flammulina velutipes	—	7200	AF030877	Hughes & al., unpub.

Gloiocephala epiphylla	USA	DED5971	DQ097357	Binder & al. 2006
Hymenopellis radicata	Sweden	TENN62837	GQ913377	Petersen & Hughes 2010
Laccariopsis mediterranea	Italy	MCVE23445	JX271808	Vizzini & al. 2012
Mucidula mucida	Austria	TENN59324	GQ844235	Petersen & Hughes 2010
Paraxerula americana	USA	DBG21746	HM005143	Petersen & Hughes 2010
Rhizomarasmius pyrrhocephalus	USA	TENN51091	DQ097369	Binder & al. 2006
Rhodotus palmatus	Czechia	PRM889504	KC179739	Tang & al. 2014
Strobilurus conigenoides	USA	TENN61318	GQ892821	Petersen & Hughes 2010
Xerula pudens	Estonia	TUF117431	UDB031394	UNITE
Outgroup				
Crinipellis scabella	—	CBS243.53	MH857177	Vu & al. 2019
Marasmius rotula	Denmark	NN005958	JN943598	Schoh & al. 2012

* Personal herbarium of Sara Landvik

other specimens, distributed widely throughout the Northern Hemisphere: from Alaska to Greenland in North America, and from Scandinavia to Kamchatka in Eurasia, with additional European collections from Czechia and Italy; the Italian collection was less than 200 km from Boboli Gardens, site of the collection Micheli used for his illustration that is now the lectotype of *A. umbellifer*. Two relatively recent collections from Öland failed to yield amplifiable DNA, but collections from nearby Saaremaa and the west coast of Estonia produced sequences that fell into the same clade. The species is sister to a small clade of five collections, with which it shares morphology (as evidenced by the application of the same name), distribution in Lapland, and substrate preference (fallen leaves of *P. tremula*).

Molecular studies enabled us to settle Redhead & Kuyper's unresolved concerns about the shape of the pilei of their selected lectotype, compared to the protologue description. Among the 21 specimens conspecific with our Lapland collection, we were able to locate photographs of three, in addition to our own. These photographs, together with Micheli's illustration (Fig. 8), reveal that during its development from grain-like pinhead-shaped immature pilei to applanate ones at maturity, the pileus of this short-lived species goes through near-hemispheric, convex, and plano-convex stages. AV noted several convex and plano-convex pilei the first day they appeared—the stage congruent with Micheli's illustration—and returned to photograph them the next day—capturing mature applanate pilei congruent with the stage described by Linnaeus. The species seems to be a generalist with many deciduous hosts, collected from the same year's dead leaves, litter, or even wood. Of the hosts, *P. tremula* occurs on

Fig. 7. *Owingsia* species from three of our four species clades.
Owingsia umbellifera, Estonia: A. TUF118453; B. TUF118289; C. TUF106979.
Owingsia sp. 1, Estonia: D. TUF118729; E. TUF118324.
Owingsia sp. 2, Canada: F. UWO-F3413. Scale bars = 10 mm.
Photos: A–E, courtesy of Vello Liiv; F, Greg Thorn.

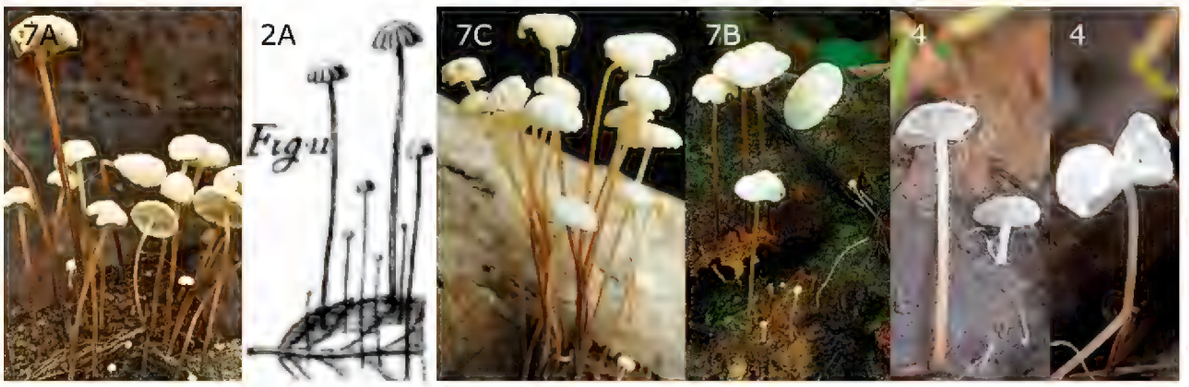

FIG. 8. Sequence-identified collections of *O. umbellifera* taken from FIGS 4A, 7A, B, C (source identified in left upper corner), together with the lectotype for the species (from FIG. 2A) for comparison of pileal shape. The cap begins as a near-globular pinhead atop an immature stem (7A , B, lower middle), opens up to small hemispheres (7A middle, 7C lower middle), then becomes convex (7A, C) to plano-convex (7A, B), and finally flattens out to applanate in maturity (4). Note that all the earlier stages are accurately depicted on the lectotype. Also note the plications and scalloped margins of the cap, and relatively sturdy long stems, all accurately captured by Micheli.

land between the Mediterranean and the Barents Seas, the documented European North-South range of the fungus.

COMMENTS

Not only is our collection the most common in its complex of similar species, but photos of the clades (Fig. 7) suggest that it also has the longest stipe of these clades (i.e., most closely resembles the illustrations chosen by Linnaeus to show this character of his species). These two observations suggest that of the group of similar species, this was the most likely one seen and described by Linnaeus with the name *A. umbellifer*.

Initially we recombined *A. umbellifer* into *Marasmius*, but discussion during the review process convinced us that this was less than optimal, given the phylogenetic distance of *Marasmius* s. str. from this genus. In an unpublished Master's thesis, Owings (1997), using the LSU marker, first showed that *Marasmius*, as known at that time, was a polyphyletic genus, and, inter alia, that species of *Marasmius* sect. *Epiphylli*, along with some other genera, followed a divergent evolutionary pathway to the *Physalacriaceae*. She reported these findings with her supervisor in an abstract (Owings & Desjardin 1997), and her observations have been confirmed in various LSU-based studies of the *Physalacriaceae* (e.g., Wilson & Desjardin 2005, Ronikier & Ronikier 2011, Vizzini & al. 2012, Jenkinson & al. 2014). Multilocus analysis by Matheny & al. (2006) confirmed that *Marasmiaceae* and *Physalacriaceae* form separate provisional families arising in what they named the marasmioid clade, one of six major clades of *Agaricales*. Classifying *Marasmius*, Kühner (1933) named "*M.* sect. *Epiphylleae*", forming the name from *M. epiphyllus*, which he placed in the section. The Code (Art. 10.8) considers such implicit assignment of type species valid; Kühner's sectional epithet must be corrected to a masculine plural

adjective, agreeing with the masculine genus (Art. 21.2), thus, *Marasmius* sect. *Epiphylli*.

A new genus typified by *Agaricus/Marasmius epiphyllus* would require a satisfactory typification of that species. A beginning was made by Singer (1969), who described *M. epiphyllus* as heterogenous, discussed two taxa, and then stated that he had no hesitation to designate one collection from Ulfült near Femsjö as topotype for *M. epiphyllus*. This is a bit puzzling, because topotypes have no nomenclatural significance, and are not DESIGNATED, but are what they are by definition: the same species from the same site where the type was collected. In this case, neither, Persoon, who described *Agaricus epiphyllus*, nor Fries, who sanctioned that name and subsequently transferred it to *Marasmius*, cited a type collection, making it impossible to meet the definition. Fries did indicate that he had seen the species (v. v.), but the Code requires that a precise specimen be identified by the author for valid typification (Art. 7.11). As opposed to topotypes, neotypes must be designated. Singer did not DESIGNATE the cited specimen as neotype, but rather stated, "we [i.e., I] ... RECOMMEND it as neo-type of the species." Characteristically, Singer's type designations are brief, clear, and unequivocal, suggesting that such certainty was not his intent in this case.

Erecting a new genus with a new name and its own type species circumvents the above concerns nicely, and also avoids the need to reconcile some additional concerns. For example, Desjardin (1989) described lack of rhizomorphs as one of the characters of *M.* sect. *Epiphylli*, but rhizomorphs are very prominent in FIG. 4. Needless to say, the simplicity of erecting a new genus, suggested and/or approved by our reviewers, appealed to us. We shall describe briefly the new genus, *Owingsia*, recognizing that a genus created for nomenclatural convenience, without resolving its taxonomy, will not satisfy all taxonomic expectations until its taxonomy becomes settled. Taxonomic study to resolve *Marasmius* sect. *Epiphylli* is a major undertaking, requiring familiarity with the group, wide sampling and sequencing, reconciling several old names by typification, synonymization, or other means, and probably needs a global approach. For example, the different topology we noted with Bayesian and maximum likelihood analyses suggest the need for including more North American specimens, ideally with an attempt to sequence the type of *Marasmius subvenosus* Peck, and the need to include more (conservative) genetic markers in the analysis. Such work, best done by experts familiar with these species, is well beyond the scope of the stated narrow aims of this nomenclatural study. Our only reason to erect a new genus at this time is to accommodate the new combination for *A. umbellifer* in a place more logical than *Marasmius*.

NOTE: We are **NOT** suggesting that *Marasmius epiphyllus* is now known as *Owingsia umbellifera*. As we have seen, collections in three of the four clades we have identified in the genus, have been labeled as *M. epiphyllus*. The fourth, now identified tentatively as *M. subvenosus*, was initially also thought to be *M. epiphyllus*. The nature and relationship of the current *M. epiphyllus*

to *O. umbellifera* and the other species in the new genus is unknown. It will only be revealed once the taxonomy of *Owingsia* is worked out and each of its species given a modern sequenced type. Without typification, we are unable to circumscribe *M. epiphyllus* and cannot say what the species is or how it differs from the others. What we can say at this time, is that because our limited sequencing produced four clades to which the epithet has been applied, likely the taxonomists who undertake this task would have ample latitude to retain the epithet *epiphyllus* without conflict.

Taxonomy

Owingsia I. Saar, Voitk & Thorn, in Voitk, Thorn & Saar, Mycotaxon 137(4): 651 (2023)
MB 845593

= *Marasmius* sect. *Epiphylli* Kühner [as "*Epiphylleae*")], Le Botaniste 25: 93. 1933.

Differs from *Marasmius* s.str. by its acollariate attached lamellae, stipe with visible vestiture, lack of broom cells, prominent cystidia, and molecular data.

Type species: *Owingsia umbellifera* (L.) Voitk & al.

Etymology: Named after Pamela Owings, who first described the divergence of *Marasmius* sect. *Epiphylli* from the evolutionary pathway of the core *Marasmius* group.

Basiomata of the four putative species clades that nestled in *Owingsia* by our ITS data (Fig. 7) are all small (cap diameter seldom over 10 mm) and whitish, with all tissues inamyloid, non-dextrinoid, and share the following characters: pileus segmented, somewhat parasol- or windmill-shaped, going through an initial stage of decreasing convexity, usually becoming plane at maturity; lamellae reduced to widely spaced, acollariate, developing fold- or vein-like anastomosing ridges, developed lamellae approach the stem for a broad attachment, but within a fraction of a mm develop a sharp notch, attached to the upper stipe less broadly; stipe usually long (>2.5× cap diameter), central, pruinose, insititious; basidiospores fusiform, hyaline, without iodine reactions; cystidia present on lamellar sides and edges, on stipe, and on pileus, narrowly fusiform to narrowly lageniform, mostly with a long neck, thin-walled; pileipellis hymeniform, made up of clavate or broadly clavate, slightly to distinctly thick-walled cells; stipitipellis a cutis; epiphyllic on fallen deciduous leaves and small deciduous or herbaceous litter. Phylogenetically, our ITS data (Fig. 6) show that the genus arises from a well-supported pathway within the *Physalacriaceae* (distant from *Marasmius*, type species *M. rotula*).

SP1: ESTONIA, Saare, Saaremaa, Harilaid, 02.11.2011, Vello Liiv (TUF118324; UNITE UDB015484); near Viidu, mixed forest, on leaves of *Populus tremula*, 08.10.2013, Vello Liiv (TUF118729; UNITE UDB019538); FINLAND, Outer Ostrobothnia, Ylitornio, S end of Kuusikkorommas, S part of the nature protection area, rich spruce-dominated mixed forest on calcareous ground, on leaves of *Populus tremula*, 27.09.2014, Esteri Ohenoja, Taina Romppanen, Lasse & Marja Tuominen

(OULU10007053; UNITE UDB07672481); Sompion Lappi, Pelkosenniemi, Jaurujoki E, Kuotelonjoki SW, 26.08.1994, Ulla Nummela-Salo, Pertti Salo (OULU-F-24077; UNITE UDB07672486).

SP2: CANADA, Ontario, Essex County, Point Pelee National Park, West Beach, 41.9266 -82.5138, 176 m a.s.l., on fallen leaflets and rachis of *Ptelea trifoliata* in open grass-oak-juniper savannah on shoreline, 05.10.2020, P. Kelly, N.M. Weerasuriya & R.G. Thorn, RGT201005/08 (UWO-F3413; OP290397; culture DAOMC252643).

Comment. Formation of a distinct genetic clade within *Physalacriaceae* and congruence with *Marasmius* sect. *Epiphylli* has been confirmed by previous work (vide supra). A fuller and more exact concept of the genus awaits further taxonomic work within the group, including typification of its species.

Owingsia umbellifera (L.) Voitk, I. Saar & Thorn, in Voitk, Thorn & Saar, Mycotaxon 137(4): 652 (2023) Fig. 4
MB 845594

≡ *Agaricus umbellifer* L. [as "*umbelliferus*"], Sp. Pl. 2: 1175. 1753 (nom. sanct., Fr., Elench. Fung. 1: 22. 1828).

Typification: **Holotype**, none. **Lectotype** Tab. 80, Fig. 11 (Micheli, Nov. pl. gen. (Florentiae), 1729) designated by Redhead & Kuyper (Arctic and Alpine Mycology II: 319. 1987). **Neotype** and **isoneotype** designated by Voitk et al. 2023a **not Code compliant**. **Epitype** [IF 901100; designated by Voitk et al. 2023b], Norway (Lapland), Finnmark (now Troms og Finnmark), Rafsboten, Tverrelven, 70.0159°N 23.5587°E, 47 m asl, in mixed woods on fallen leaves of *Populus tremula*, leg. Andrus Voitk 06.10.04. av01 (O-F-76596; **isoepitype**, TUF117828; UNITE UDB0799033).

Macroscopic. Basidioma: small, white, epiphyllic, with a thin, translucent, flat, umbrella-like pileus on a long stipe; pileus: 4–8 mm in diameter, membranaceous, translucent, going through various stages of decreasing convexity to become plane at maturity (Figs 4A, 7A, 8 B, C), drooping during drying (Fig. 4C, 7A, C), but on rehydration flattening out again, umbrella-like segmented, white; lamellae: distant, occasionally reduced, develop cross-veining anastomoses with age, approaching the stem for a broad attachment, but form a deep notch a fraction of a mm away from the stem (possibly by separating from it) to attach more narrowly to the upper stipe, white, acollariate; stipe: 15–26 mm high and about 1 mm wide, evenly cylindrical, straight or occasionally bent, minutely flocculose, white, with some yellow to straw colour rising from the base with maturity, insititious, usually arising from leaf veins, associated with several white rhizomorphs or sterile stipes at maturity (Fig. 4A, B); spore print: white.

Microscopic. Basidiospores: (n = 50; 3 basidiomata, 2 collections, 2 observers) 7.7–13.5 × 3.5–6.7 µm (average 11.8 × 5.1 µm), Q = 2.0–2.9, (average 2.3), ellipsoid-lacrymoid, hyaline, inamyloid; basidia: (n = 7) 8–11 × 42–54 µm, 4-spored, about 15% 2-spored (Fig. 4C); cystidia: plentiful and pleomorphic (Fig. 4D); cheilo- and pleurocystidia: similar (n = 18) 25–42 × 4.5–67.3 µm (average 33.5 × 5.7 µm), narrowly fusiform to lageniform, mostly with a long neck, thin-walled (Fig. 4E, F); pileocystidia: slightly larger but otherwise

similar to hymenial cystidia (n = 12) 27–44 × 5.3–8.5 µm (average 38 × 6.6 µm), narrowly fusiform to narrowly lageniform, mostly with a long neck, thin-walled (Fig. 4G); caulocystidia: (n = 8) 20–26 × 4–6 µm (average 24 × 5 µm), fusiform to lageniform, thin-walled to slightly thick-walled (Fig. 4H); pileipellis: hymeniform, (n = 28) 12–26 × 6–12 µm (average 19 × 10 µm), clavate to broadly clavate, slightly to distinctly thick-walled cells (Fig. 4I); stipitipellis: a cutis of hyphae, up to 3–8 µm wide; clamp connections: in all tissues.

Additional specimens examined: **ESTONIA**, Saare, **Saaremaa**, near Viidu, on rotten wood, 10.10.2010, Vello Liiv (TUF106979; UNITE UDB015277); on deciduous twigs, 28.09.2012, Vello Liiv (TUF118453; UNITE UDB018190); **Pärnumaa**, Nigula mire, swamp forest, on fallen leaves of *Populus tremula*, 03.10.2011, Vello Liiv (TUF118289; UNITE UDB015455). **FINLAND**, Inarin Lappi, Utsjoki, Kenesjärvi, 14.09.1972, Martti Ohenoja (OULU-F-16606; UNITE UDB07672483); Perä- Pohjanmaa, **Lapland**, Tornio, Kalkkimaa SE, near Alatolo farm, S side of the road, deciduous forest (*Alnus*), 16.09.1986, Esteri Ohenoja, Tuula Vuorinen (OULU-F-16597; UNITE UDB07672480); Sompion Lappi, Pelkosenniemi, Suvanto NW, Niskakorpi, Niskaojan varsi, N-side of road, 11.09.1985, Esteri Ohenoja (OULU-F-16603; UNITE UDB07672482); Pelkosenniemi, Siulioaapa NE, 25.08.1994, Ulla Nummela-Salo, Pertti Salo (OULU-F-24076; UNITE UDB07672485). **NORWAY**, Troms, Lullesletta, rich deciduous forest along a brook, 19.08.1992, Esteri Ohenoja OULU-F-21543; UNITE UDB07672484). **SWEDEN**, Norrbotten, **Piteå**, Mjöviksmoåsen, 10.1982, Brigitta Öster (UPS-F-740369; UNITE UDB07672488).

Ecology: saprobic generalist, collected from dead leaves (usually arising from the midrib or other leaf veins) litter (small branches twigs and bark), or even wood. Documented host species: *Acer pseudoplatanus* L., *Alnus* Mill. sp., *Castanea sativa* Mill., *Crataegus* Tourn. ex L. sp., *Fagus* L. sp., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Petasites kablikianus* Tausch., *P. tremula*, *Quercus ilex* L, *Q. pubescens* Willd., *Q. robur* L., and *Q. rubra* L.

Habitat: deciduous and mixed woods.

Phenology: September–October; epitype appeared after first night frost.

Distribution: So far confirmed from the Northern Hemisphere, both sides of both North America and Eurasia; in Europe from the Mediterranean to the Barents Sea.

Comment. The macroscopic description of *O. umbellifera* is based primarily on the epitype specimen. To spare type material, microscopic observations were augmented by or based entirely on sequence-confirmed conspecific material. A fuller species concept is expected to evolve as *Owingsia* and its species get resolved taxonomically.

Note: The major nomenclatural error of our original report (Voitk et al. 2023a) has been corrected here, as per the correction reported in the nomenclatural novelties of Index Fungorum (Voitk et al. 2023b). Because the Code does not permit superseding the lectotype by Redhead & Kuyper, the neotype erected

in the original report was not Code compliant. With this publication we retain the Redhead & Kuyper lectotype, withdraw the Voitk et al. 2023 neotype, and declare the same collection (O-F-76596) as **EPITYPE** for *O. umbellifer*.

SEARCH FOR A NEW NAME FOR AM-MIN

We began this quest by reviewing descriptions of AM-MIN culled from the cited major workers and those they have quoted, MycoBank and Species Fungorum, appropriate texts, and other sources. FIGURE 9 is a composite plate of some illustrated candidates for AM-MIN from the past, many used in past typification attempts, labelled with year of publication, author, and binomial (where available), all cited in the legend. The plate is arranged in rows to facilitate the discussion around the search for the optimal name. Note that the pleomorphic appearance of the species on this plate resembles that seen on modern photos of AM-MIN (FIG. 1).

The upper row, FIGS 9A–D, predate the use of binomial names; FIG. 9A was drawn but not named or described, and FIGS 9B–D were identified by a phrase name. All appeared before 1753, i.e., before the starting-point of valid fungal nomenclature (Art. F.1). Hence, even had they been named, the names would be considered unavailable.

The second row of FIG. 9 shows two taxa with a striking resemblance to AM-MIN. Figure 9E, *A. niveus* Vahl, is an illegitimate name because the epithet was already in use in *Agaricus*, and is thus not available. Figure 9F, *A. valgus*, is unsanctioned, and, therefore, plays no role in the nomenclature of AM-MIN, so long as a fitting sanctioned name is available.

The third row, FIGS 9E–G, show three illustrations by Bolton of *Agaricus cespitosus*, minimally rearranged for space. FIGURES 9G & H come from two volumes in a prepublication folio manuscript, handwritten and hand-painted (Bolton 1784, 1786), each obviously based on a different collection. FIGURE 9I shows Bolton's definitive copper plate, used to illustrate his formal printed description of the species (Bolton 1788), obviously based on FIG. 9H. These illustrations were used by Voitk (2022) in a detailed discussion of the synonymy of *A. cespitosus* with *A. oniscus* Fr. nom. sanct., and their conspecificity with AM-MIN. Namely, 30 years after Bolton described AM-MIN with the name *A. cespitosus*, Fries (1818) described *A. oniscus*, stating that this new name was to replace all synonyms (including *A. cespitosus*, the only name he cited). Ordinarily a new name for a legitimate earlier name would be deemed illegitimate as superfluous, but Fries described *A. oniscus* again in his Systema Mycologicum (Fries 1821), giving *A. oniscus* sanctioned priority over *A. cespitosus*. Their synonymy was formalized by declaring the illustration shown in FIG. 9H as lectotype for *A. cespitosus* and FIG. 9I as lectotype for *A. oniscus* (Voitk 2022). Because FIG. 9H was used to make FIG. 9I, the species are homotypic. [We note that due to a typographical error, Voitk (2022) listed the date of publication of Bolton's painting chosen for lectotypification of *A. cespitosus* as 1784, instead of 1786.

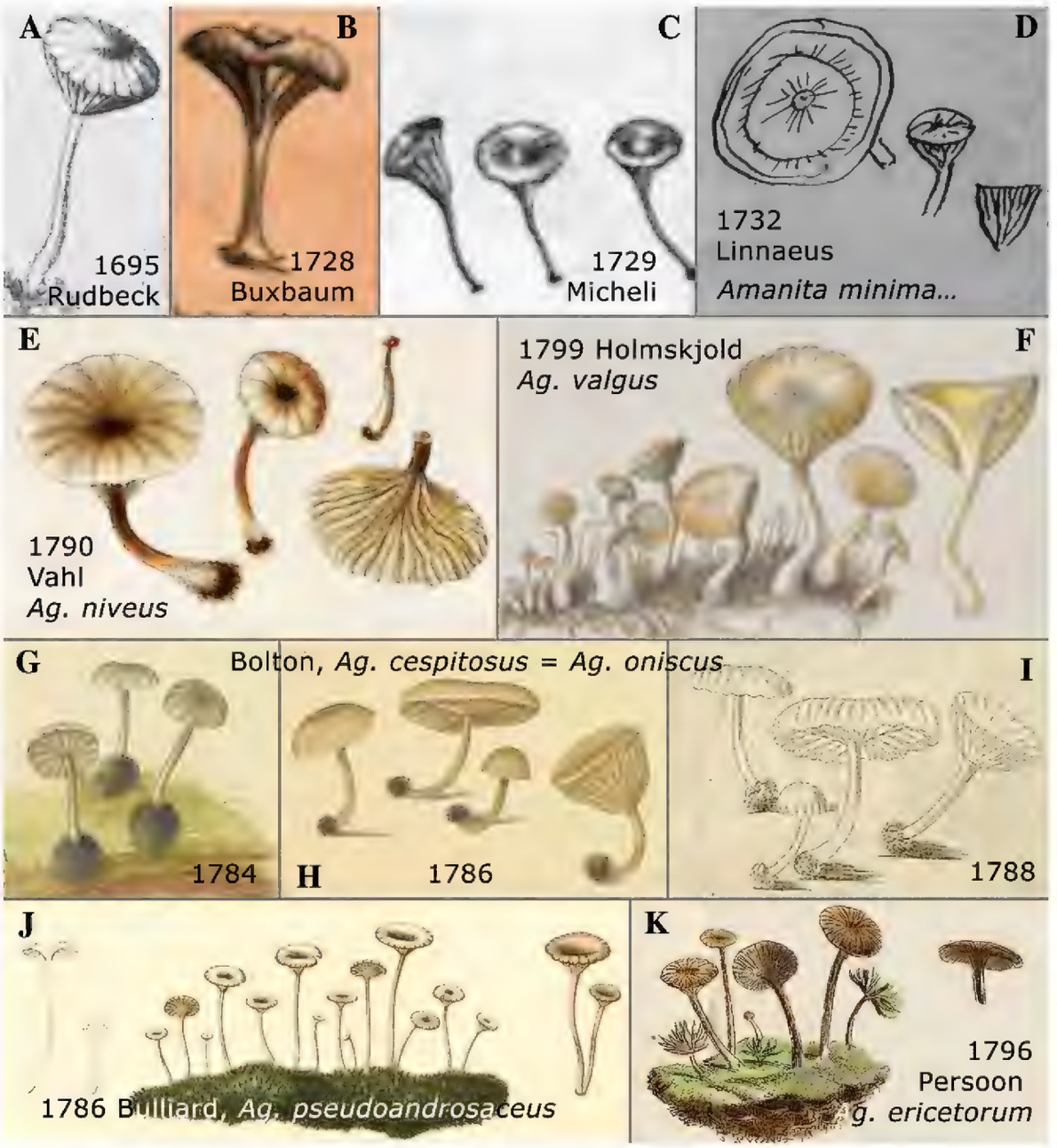

FIG. 9. Composite plate of some real or potential AM-MIN synonyms. Morphological variation akin to that seen on FIG. 1. A. Illustration by Rudbeck (Anfält 1987) of a specimen resembling AM-MIN—same as FIG. 2E, above; no name or description given; B. Illustration by Buxbaum (1728) of a specimen resembling AM-MIN, phrase name given; C. Illustration by Micheli (1729) of a specimen resembling AM-MIN—same as FIG. 2C, above; phrase name given; D. Illustration by Linnaeus (Fries 1913) of a specimen resembling AM-MIN—same as FIG. 2F, above; phrase name given; E. Protologue illustration by Vahl (1790) of *Agaricus niveus*; F. Protologue illustration by Holmskjold (1799) of *Agaricus valgus*; G. Prepublication illustration by Bolton (1784) of *Agaricus cespitosus*, also labelled *Agaricus umbelliferus*; H. Prepublication illustration by Bolton (1786) of *Agaricus cespitosus*, selected as lectotype for *Agaricus cespitosus* (Voitk 2022); I. Protologue illustration by Bolton (1788) of *Agaricus cespitosus*, selected as lectotype for *Agaricus oniscus* by Voitk (2022); J. Protologue illustration by Bulliard (1786) of *Agaricus pseudoandrosaceus*, the middle group on a moss cushion selected as lectotype for *Agaricus ericetorum* by Redhead & Kuyper (1987); K. Protologue illustration by Persoon (1796) of *Agaricus ericetorum*.

The correct year appears elsewhere in Voitk's article, and both the description of the image and the citation of source are clear, making the required correction patent.] Although Fries declared that the sanctioned *A. oniscus* was to replace all synonyms (i.e., past, present, and future) for *A. cespitosus*, it takes effect on the publication date of its protologue, 1818. This gives any sanctioned name for Am-min published before 1818 priority over *A. oniscus*.

The fourth row, Figs 9J & K, are protologue illustrations for the earliest description of Am-min, *A. pseudoandrosaceus* Bull. (Bulliard 1786), and its declared synonym, *A. ericetorum* Pers., described ten years later (Persoon 1796). Again, ordinarily this later synonym would be a considered a superfluous name, but when Fries described the taxon in his 1821 Systema, *A. ericetorum* became sanctioned, taking precedence over Bulliard's name. This ascension to precedence suffered a little transient hiccough because earlier versions of the Code did not extend sanction to names of lichenized fungi. Only after the Code extended the same sanctioning rules to names of lichenized basidiomycetes, and Am-min was considered one of them, did *A. ericetorum* gain its priority over *A. pseudoandrosaceus*. The effective publication of this sanctioned name was 1796, two years before *A. cespitosus*, and 22 years before the sanctioned *A. oniscus*, giving *A. ericetorum* priority. Both *A. pseudoandrosaceus* and *A. ericetorum* were lectotypified (Redhead & Kuyper 1987) with the central light-coloured basidiomata on a moss cushion of Fig. 9J, Bulliard's protologue illustration, making them homotypic, thus formalizing Persoon's intended synonymy. One earlier lectotypification (Singer 1961) with a collection made by Persoon was rejected by Redhead & Kuyper because it had not been seen by Bulliard (i.e., could not be part of Bulliard's original material), and was undated, thus lacking evidence that it was part of Persoon's original material. Hence, Redhead & Kuyper's lectotypification is the earliest, and should be followed, according to the Code, now that *A. umbellifer* has been recombined in accordance with its protologue as *Owingsia umbellifera*. In other words, the sanctioned *A. ericetorum* regains its priority (Arts 11.4, F.3) as the basionym for Am-min. So long as *A. pseudoandrosaceus* and *A. ericetorum* are homotypic, attempts to treat them as separate taxa are erroneous (e.g. Singer 1961, Moser 1983), as is the combination of *A. pseudoandrosaceus* to *Mycena* (Bi & al. 1987). As mentioned earlier, because *A. ericetorum* and *A. umbellifer* represent two different species, designating specimen 1753 from Fungi Exsiccati Suecici neotype for both by M. Lange (1981), and epitype for both by Jørgensen & Ryman (1994), is now without standing (Arts 9.18 and 9.20).

The above paragraph is but a condensed review of a very complex nomenclatural story involving these taxa. Much more detail is available in Redhead & Kuyper (1987), Redhead & al. (2002), and the many references cited by these authors. In short, Redhead & Kuyper (1987) have already identified an appropriate name for Am-min with a lectotypification, subsequently rejected by Redhead & al. (2002). Should we wish to reinstate it, our task is to ensure

that this earliest available name for Am-min still remains appropriate. Persoon cited *A. pseudoandrosaceus* as a synonym, but there must be no conflict between the two protologues, including all associated original material, for his opinion to be valid. There is an obvious colour difference between the two protologue illustrations, Persoon's being much darker than Bulliard's. This discrepancy is not evident in their protologue descriptions, suggesting a colouring artefact, and making both compatible with each other and with Am-min. Bulliard described *A. pseudoandrosaceus* as white to ash grey (gris cendré), occasionally yellowish white. Persoon described *A. ericetorum* as light grey (fragile griseo), and quoted Sibthorpe's (1794) description, lightly dusky (subfusco). The varying references to light grey are compatible with a moist translucent whitish cap, a common appearance of Am-min—see Fig. 9G, and a detailed discussion with contemporary photos of this by Voitk (2022). Persoon described the base of the stipe as white, covered with tomentum, and the lamellae as whitish. These descriptions are not congruent with the dark brown basidiomata of Persoon's illustration, again implicating technical problems with rendering accurate colour. Although Persoon did not comment about the colour of his illustration (he may not have seen it at the time of writing), he did mention that the artist had failed to illustrate the shape of the gills adequately, raising some questions about the accuracy of the illustration even before it was painted.

We polled five arctic-alpine experts familiar with Am-min (Torbjørn Borgen, József Geml, Gro Gulden, Pierre-Arthur Moreau, Anna Ronikier) about the compatibility of Persoon's illustration with Am-min, and not surprisingly, all found the basidiomata dark. Two thought this was incompatible, without further comment, one specified that the image would be very accurate if it were of lighter colour, and two had no hesitation to accept them as is: one of them volunteered that Am-min is so pleomorphic that its spectrum even encompasses the basidiomata on Persoon's image, while the other said that the green ground cover almost certainly represented a botryoid lichen thallus, and, more significantly, that basidiomal colour should be disregarded entirely, because of the known inaccuracy of hand painting and post print changes. Thus, the only problem with the image identified was dark colour, which found no support in the descriptions, and seems best ignored. That the illustrations darkened with time was also the observation of Singer (1961). We note that just as Redhead & Kuyper selected only light basidiomata for typification, when choosing a lectotype for *A. oniscus*, Voitk (2022), on encountering a wide variation in colour of hand-painting the same engraving of *A. cespitosus*, specified an unpainted one for typification. Other examples abound. For instance, images of the white *A. porcellaneus* Schaeff. published by Schaeffer (1774), subsequently appear from light to very dark brown in different issues of Bulliard's Herbier de la France, vol. 1 (Bulliard 1780).

Our conclusion was that the most likely species intended by both Bulliard and Persoon was Am-min, making them synonyms. Although other explanations

are possible, support for those seems considerably more tenuous. Therefore, we have no hesitation rejecting the rejection of Redhead & al. of Redhead & Kuyper's lectotypification of both *A. pseudoandrosaceus* and *A. ericetorum*—in other words, reinstating Redhead & Kuyper's lectotypification of both *A. pseudoandrosaceus* and *A. ericetorum* with Bulliard's protologue illustration of *A. pseudoandrosaceus*.

Taxonomy

Lichenomphalia ericetorum (Pers.) Voitk, Thorn & I. Saar, in Voitk, Thorn & Saar, Mycotaxon 137(4): 652 (2023), Figs 1, 10 MB 845595

≡ *Agaricus ericetorum* Pers., Observ. Mycol. 1: 50. 1796 (nom. sanct., Fries, Syst. Mycol. 1: 165. 1821)
≡ *Agaricus pseudoandrosaceus* Bull., Herb. France 6: tab. 276. 1786.
Typification: **Holotype**: none designated or preserved. **Lectotype** [MBT593068, Redhead & Kuyper 1987], Bulliard tab. 176, 1786, *Agaricus pseudoandrosaceus*. Herbier de la France 6: tab. 276. **Epitype** [MBT10013917], Estonia Tartumaa, Järvselja, 58.2668°N 27.3179°E, 25.08.2016, V. Liiv (TUF120612).
= *Agaricus oniscus* Fr., Observ. Mycol. 2: 209. 1818 (nom. sanct., Fries, Syst. Mycol. 1: 172. 1821)
≡ *Agaricus cespitosus* Bolton, Hist. Fung. Halifax 1: 41, pl. XLI, Fig. C. 1788.

Misapplications:
≠*Agaricus umbellifer* L., Sp. Pl. 2: 1175. 1753.
≡ *Amanita umbellifera* (L.) Roussel, Fl. Calvados: 34. 1796.
≡ *Merulius umbellifer* (L.) With., Arr. Brit. Pl., Edn 3, 4: 147. 1796.
≡ *Omphalia umbellifera* (L.) P. Kumm., Führ. Pilzk.: 107. 1871.
≡ *Omphalina umbellifera* (L.) Quél., Enchir. Fung.: 44. 1886.
≡ *Clitocybe umbellifera* (L.) H.E. Bigelow, Can. J. Bot. 37: 773. 1959.
≡ *Lichenomphalia umbellifera* (L.) Redhead & al., Mycotaxon 83: 38. 2002.

Capsular epitype description (Fig. 10)

Macroscopic: Basidiomata omphalinoid. Pileus up to 20 mm, low convex to plane, centre often umbilicate, smooth, margin crenulate, translucently striate, pale yellow. Lamellae deeply decurrent, sometimes forked, distant, concolorous with pileus or paler. Stipe 10–20 × 1–2 mm, smooth, dry, yellowish.
Microscopic: Basidiospores 7.5–12 × (4.8–)5.3–8.8 µm, mean 9.9 × 6.8 8 ± 1.4 µm, Q = 1.3–1.6, mean 1.4 ± 0.1; hyaline, inamyloid, broadly ellipsoid to ellipsoid. Basidia 30–32 × 9–11 mm, 4-spored. Cystidia and clamp connections absent.

Note: Fig. 1 and its legend discussion give an overview of the pleomorphic spectrum of the species.

DISCUSSION

Stability

Our findings are factual, but our solution is a matter of opinion. The Code specifies that a misapplied name, producing major conflict with its protologue,

FIG. 10. Epitype of *Lichenomphalia ericetorum* (TUF120612) in situ. Photo: Vello Liiv.

can and should be corrected, but also advocates against change if it destabilizes established custom. Conflict, stability and established custom are matters of judgment, opinion or belief, not determined by the Code, or verifiable by scientific means. We lack the enthusiasm of some onomasts for nomenclatural stability at all cost, and believe that there should be no hesitation to correct application of names producing serious conflict with their protologues. In these times of great phylogenetic discovery, names change almost daily. Correcting a few discordant nomenclatural misapplications accounts for a negligible proportion of these changes. We find it difficult to take seriously views that these few changes pose a genuine threat to nomenclatural stability. Instability should not be confused with deviation from personal practice or preference. Our experience does not confirm undue hardship from changing the name of AM-MIN from *Omphalina ericetorum* to *Lichenomphalia umbellifera*, and we expect no adverse effects this time either. Twenty years of stability does not seem long in a 270-year history. While it is correct that various forms of *umbellifer* have been applied to AM-MIN even before the last 20 years, it is difficult to speak seriously of "established custom" for a species that has been known by at least 21 separate subspecific and 17 specific epithets, dispersed through 19 genera! Applying the name of a long-stemmed epiphyllic saprobe to a short-stemmed turficolous mutualist in the interests of fostering "stability" will only foment long-term instability, prompting each new generation to reattempt correction. Maintaining a name in conflict with its protologue will make Redhead & Kuyper's attempt in 1987, followed by Voitk,

Thorn & I. Saar's in 2023, the first two in a perpetual pattern until the conflict is eliminated or a motion to conserve is approved. To resolve each misapplied name with a motion to conserve seems excessive, especially when a concinnous solution is available, with minimal "unsettling" effects, which will be forgotten in less than a decade.

Involving a species from *Marasmius* sect. *Epiphylli* cannot destabilize that group, whose taxonomy is already in an unresolved state of flux: the section does not belong in *Marasmius*, but a group in a more appropriate location has not been named. The creation of *Owingsia* will help stabilize that state. It is reassuring to note that we are not alone in that opinion, but reviewers, editors, other consultants and advisors actually suggested we create a new genus, and it is not insignificant that two internal reviewers supporting this step were among the leading marasmiologists from two continents.

Synonymy of citations

An interesting observation during this work was that reassessment of how to interpret citations may be helpful. Even citing personal findings is subject to error. We have all misidentified fungi, not only in the field, but also after further study. This is why mixed type collections, requiring splitting and lectotypification, are not rare. Mycologists turn to fungaria for reliable specimens, and to genetic depositories for reliable sequences, but to neither for reliable names, often considering them tentative placeholders, awaiting definitive determination. In this study, we saw that although Linnaeus produced a very clear species concept of *A. umbellifer*, the Kalmar sighting (Linnaeus 1741 & 1745a) seemed to differ from the remainder in some regard. We agree with Redhead and colleagues that descriptions of *A. umbellifer*, *A. pseudoandrosaceus*, and *A. ericetorum* likely included elements from more than one species. In fact, the relatively recent ability to identify evolutionary pathways has made reports of cryptic species hiding in complexes under one name a frequent occurrence. It is likely that *Owingsia*, so far containing four clades, all containing specimens identified initially as *M. epiphyllus*, will prove to be another such example. That most, if not all, taxa described a century or more before our technological advantages, include elements of more than one species should be accepted as a given.

Identification error rate becomes magnified when citations of identifications by other workers are automatically accepted as synonyms. This is particularly true if the opinion of synonymy is formed from laconian descriptions plus illustrations, where available, without examination of the specimens, and is based on concepts, customs, knowledge, and technology over two centuries old. Some of the difference may be seen in this article: word count for our description of *O. umbellifer*, a known species with a name in use over 270 years, excluding authorities, typification, etymology, synonymy, additional specimens examined, and comments, is 458. In contrast, the three phrase names used by Linnaeus to describe what he thought to be the same species averaged 9.3 words; the

amount of illustration (in situ macroscopic images of four collections, showing the full range of development, macroscopic image of a dried collection, several microphotographs, sequence-confirmed distribution in Lapland and around the Baltic Sea, and phylogenetic relationship) bears no comparison to what was available to Linnaeus.

To then extend synonymy to citations by the sanctioning author further increases the likelihood for error manyfold: without examining either the author's specimen or the specimen he cites, a sanctioner cannot be expected to form consistently accurate opinions of their identity, let alone true synonymy, from his desk. As long as such errors can be corrected, making the sanctioner's citations a valid alternate source for original material may produce a felicitous selection, where the author's material falls short (e.g., Stadler & al. 2014) or is missing. However, legislating that such material, with a built-in markedly elevated likelihood for error, is an OBLIGATORY choice for typification (Art. 9.13, Art F.3.9), and cannot be superseded because "cited ... illustrations" [including those cited by the sanctioner] "are part of the protologue and cannot be in serious conflict with it" (Article 9.19, Note 7), may cause problems, when there is no specimen or diagram from the author. Absence of conflict is not the same as claiming (or even legislating) that it is (be) absent. We shall examine this with a discussion of *A. capillaris* Schumach., the current *Mycena capillaris* (Schumach.) P. Kumm., not so much because this rather straightforward concept requires an example to understand it, but rather because the acceptance of Micheli's illustration as lectotype for *A. umbellifer* makes this matter relevant.

> Namely, Schumacher (1803), aware of the work of both Micheli and Linnaeus, described *A. capillaris* as a NEW SPECIES, without citing any other description, illustration, or synonym, naming it for noticeable fine hairs (capillaries) on its stipe. Fries (1821) treated *A. capillaris*, thereby sanctioning the name, citing Micheli's illustration, Tab 80, Fig. 11, a treatment of *A. capillaris* by von Haller (1769), and Schumann's protologue of *A. capillaris*. Note that von Haller quoted Micheli's text, as well as cited his same illustration. If citation means automatic synonymy, by citing von Haller's treatment, Fries placed both Micheli's text and illustration in synonymy with *A. capillaris*, not only the illustration.
>
> Because tissue is unavailable, and Schumacher did not provide or cite a diagram, current rules make Micheli's illustration the only available "original material" for *A. capillaris*. As mentioned, that drawing was designated as lectotype for *A. umbellifer*[*us*], NOT *A. capillaris* by Redhead & Kuyper (1987), although they stated that Fries's selection of Micheli's illustration to represent *A. capillaris* Schum. "was probably correct." In our original article (Voitk & al. 2023a), the general appearance of a small, whitish, long-stemmed, epiphyllic basidioma led us to agree that both Micheli's "drawing and description seem to fit that species", i.e., *A. capillaris*. Because we had (erroneously) rejected Micheli's illustration as lectotype for *A. umbellifer*, the precise fit of this diagram to a species out of our field of interest did not warrant more detailed investigation. However, now that the epitypification stands, close examination of Schumacher's protologue reveals that our eagerness to agree was too hasty. Fries (1821) erred in applying the name *A. capillaris* to Micheli's illustration or text. Schumacher's protologue, echoed by Fries, differs significantly from the taxon described and illustrated by Micheli (TAB. 5). Shumacher and Fries describe species with caps

TABLE 5 ***A. capillaris*** **comparisons**

	Schumacher	Fries	Micheli
Size	very small	small	small
Colour	white, stem darkening	white, stem apex darkening	white
Cap (progress down)	conical	acicular (acutely conical)	grain-shaped
	tubular		
	bell-shaped	bell-shaped	hemispheric
	umbilicate	umbilicate	convex
Gills	attached	attached	reduced
	distant		
Stem	long	long at least some flaccid	long erect
	most delicate		
	apex darkening		
	covered with hairs		
Season	October	September–November	May, Oct–Nov
Substrate	epiphyllic	epiphyllic	epiphyllic

that are first acutely conical, become bell-shaped, and finally umbilicate, borne on delicate or flaccid stems, while the caps of Micheli's species begin with tiny globular grain-shaped caps, expand to become hemispheric, then convex (and, as we now know, eventually applanate), without ever becoming umbilicate, borne on erect stipes. The irony of stating that this mismatched illustration "cannot be in serious conflict with" the protologue becomes painfully manifest. Such significant conflict cannot be legislated away.

Fries treated *A. umbellifer* twice, giving complexity an exponential boost. Both times Fries (1825, 1828) stated that he spoke of the species described by Linnaeus, thus giving de facto recognition to Linnaeus's original material (INCLUDING Micheli's Tab. 80, Fig. 11). In his first treatment, rather than provide a description, Fries refers the reader to Pollich (1777) as an authoritative source; the latter cited as synonyms Micheli's Tab. 80, Fig. 11, as well as three Linnaean descriptions and one by Scopoli (1772), also citing Micheli's illustration. In the sanctioning treatment (Fries 1828), he cited the 1825 treatment, thereby reinforcing citation of Micheli's 1729 description and illustration. The Code defines as original material "... illustrations ... available to the author ... at the time of ... the description ...", and as mentioned, Art. F.3.9 specifies that in the case of sanctioned names, this applies to both author and sanctioner. Thus, albeit indirectly, with his own pen Fries assigns the Micheli illustration Tab. 80, Fig. 11, as original material for the sanctioned name *A. umbellifer* seven years after he assigned it as original material for the sanctioned name *A. capillaris*. Of course, it had already been part of the original material for *A. umbellifer* ever since Linnaeus cited it as such 75 years ago.

In this case, reconciling designation of the same original material to two different sanctioned names is not problematic. Micheli's Tab. 80, Fig. 11, designated as original material for *A. umbellifer* by Linnaeus in 1753 and Fries in 1828, was declared as lectotype for the species by Redhead & Kuyper in

1987. According to the Code, this lectotypification cannot be rejected. This automatically invalidates using Micheli's illustration as original material for any name but a synonym of *A. umbellifer*. Fries did not ever claim that *A. umbellifer* and *A. capillaris* were synonyms, not then, not later, and not surprising, considering their markedly different protologues. Comparing Tab. 2 and Tab. 5 reveals that Linnaeus's *A. umbellifer* resembles Micheli's description and illustration, but differs significantly from *A. capillaris*. This solution is felicitous, because it fits well with its name, and avoids conflict between "original material" and protologue, were the other choice followed. It also fits with the principle of priority espoused by the Code. We are not aware that the Code has a direct ruling applicable to original material, but, there is a parallel precedent for two competing sanctioned names for the same species: precedence is not determined by the date of sanctioning, but by the date of valid publication of the name. Applying a similar principle here, the earlier assignment of Micheli's illustration as original material to a sanctioned validly published name should be followed, i.e., Linnaeus's citation of Micheli's illustration in 1753 for *A. umbellifer*. Hence, this illustration becomes unavailable to anyone to designate as original material for another species, including Fries's erroneous attempt in 1821. This outcome must be a welcome relief to all wishing to follow "established custom". Although Fries did not admit as much, by reassigning Micheli's illustration to *A. umbellifer* in 1828, he quietly corrected his error of 1821.

From the foregoing, it follows that we suspect that *A. capillaris* Schumach. should be typified on the basis of Schumacher's prologue alone, but rush to add that the typification of *A. capillaris*, the disposition of *A. acicularis* Hoffm., and even the question of the validitiy of the name *A. capillaris* Schumach. in light of Art. F.3.10, lie outside the scope of this work.

From a legislative viewpoint, an all-or-nothing ruling, automatically assigning synonymy to every citation is simple, but its application in every situation presents problems in real life. We do not do it now (nobody would consider that the 89 references in this paper describe synonymous taxa), so why should we treat earlier authors differently? For example, in a discussion of *A. affricatus* Fr., Fries (1818, pp. 213–214) cites *A. tigrinus* Pers. as a synonym, and then cites several other names, only to declare them different. It seems obvious that citations expressly stated as not synonymous should be excluded from automatic synonymy. But, creating several levels of citations introduces the complex matter of interpreting author intent, made more problematic because not every author is explicit about intent, even the same author does not always express it consistently, cryptic or personal expressions of intent (use of short forms, exclamation marks, etc.) can be interpreted differently or misunderstood by different observers, and intent may not be evident due to change in custom to express it. Such differences, not governable by legislation or verifiable by measurement, open the door to a variety (and difference) of opinions for exempting citations from synonymy. For example, we were able to develop what we believe to be Linnaeus's species concept for *A. umbellifer* by accepting that likely not all his descriptions or citations were synonymous (a very unlikely prospect according to current knowledge), and concentrating on common or

stressed features, rather than exceptions. Were legislation to force us to consider all as synonyms, we should be unable to reconcile a chimeric species with a convex pileus as described by Micheli together with an acute to campanulate-umbonate mycenoid pileus as described and shown by Buxbaum. Another example of author intent is demonstrated by Fries's handling of *A. umbellifer*, again perhaps a tangential concern, were Fires not the sanctioner of that name.

> Fries (1825) first mentioned *A. umbellifer* in a review of the flora around his home, Femsjö, stating that Linnaeus's synonym was surely restored, thus emphasizing that the species under discussion is that of Linnaeus. Fries's treatment was not to describe the species, but instead to cite Pollich (1777), saying the latter provided a good description of it. As mentioned, Pollich cited three Linnaean descriptions as well as the Micheli description cited by Linnaeus, and another description by Scopoli (1772). Except for Linnaeus's description from Kalmar, all specified a small white long-stemmed basidioma, to which Pollich added a description of the pileus (white, convex, becoming plane) and lamellae (white, initially arising evenly, then descending slightly to become subdecurrent at the stem). The description by Pollich, cited by Fries, and all but one description cited by Pollich were congruent with Linnaeus's protologue for *O. umbellifera*. When Fries (1828) next treated *Agaricus umbellifer*, again he did not describe the taxon himself. The heading, "*A. umbelliferus* Linn.", is a de facto citation of Linnaeus's protologue (Linnaeus 1753), to which Fries added a citation of his first treatment of the name, described above, which provided various citations of descriptions fitting that of Linnaeus. Thereafter followed two citations of works applying *A. umbellifer* to a short-stemmed (stipite brevi) species: Wahlenberg (1826), Sommerfeldt (1826), followed by citing his own treatment of *A. ericetorum* (Fries 1821).
>
> We do not share the opinion of Redhead & Kuyper (1987) that Fries indicated synonymy with all these citations. It seems highly unlikely that anyone, let alone the father of Friesian taxonomy, would proffer species with such discordant characters as long and short stems as conspecific. Instead, we conclude that the reason to mention applications of *A. umbellifer* to short-stemmed species was to alert the reader to some recent misapplications of the Linnaean name. That this is so, was made eminently clear by Fries's last citation, that of his own (Fries 1821) description of *A. ericetorum*. By preceding the citation with "V." (videre = see, view), he very specifically indicated that he did **NOT** cite *A. ericetorum* as a synonym for *A. umbellifer*, but rather invited to the reader to view (in the sense of compare and contrast) that description to judge its aptness as a synonym to the others. Surely, he did not expect the reader to judge *A. ericetorum* as an apt fit for *A. umbellifer* of Linnaeus? He knew these were different species characterized by markedly different sized stipes and markedly different substrate preferences. Rather, he invited a comparison of *A. ericetorum* to the species to which both Wahlenberg and Sommerfeldt had misapplied the epithet *umbellifer*, an obvious suggestion that *A. ericetorum* may be a better fit for **those** species than misapplied to *A. umbellifer*. Therefore, it is not surprising to learn that the descriptions of Wahlenberg and Sommerfeldt do resemble *A. ericetorum* far better than *A. umbellifer*. Redhead & Kuyper (1987), operating under earlier rules, concluded that Fries introduced a later homonym, *A. umbellifer* Fr. When Fries

(1828) sanctioned *Agaricus umbellifer*, he very definitely included elements of Linnaeus's protologue for *A. umbellifer*, including the subsequently designated type (Micheli's 1729 illustration, Tab 80, Fig. 11), also included in Linnaeus's protologue. Hence, according to the new Art. F.3.10, Fries did not create a later homonym, "Agaricus umbellifer Fries" (illegitimate under the rules of the time), but sanctioned the name *Agaricus umbellifer* L.

Nomenclature & taxonomy

Giving names treated by Persoon and Fries priority is an arbitrary nomenclatural decision to provide stability at the small expense of making a few names unavailable, which might otherwise have had a claim to precedence. This has worked very well partly due to the prowess of these workers at identification, and partly because it was strictly limited to nomenclature, a system for naming taxa. Taxonomy is a scientific discipline of ranking groups according to their relatedness. Like any scientific field, relatedness is knowledge based. Because new knowledge is always being discovered, stability in taxonomy is an unattainable goal (Turland 2019); it creates a fungible structure, whose parts (taxa) are named according to nomenclatural rules. Any stability of this system comes from nomenclature, which aims to apply infungible names [recently articulated as the "one fungus = one name" principle (Taylor 2011)]. **Synonym** is a nomenclatural term for two names that stand for the same taxon. **Conspecific** is a taxonomic term for two taxa that belong to the same species. Taxonomy, based on knowledge, provides the structure for names to be placed, but names do not determine the structure. In other words, if taxonomy shows two different individuals to belong to the same species (conspecific), the same name can be applied to both, but arbitrarily applying the same name to two individuals (synonymy) does not make them conspecific. Mandating that an illustration cited by a sanctioner is the obligatory original material for a different author's (different) species, may violate the above, converting a nomenclatural act into a taxonomically unacceptable one; synonymy can be legislated, but conspecificity can not. We accept Fries's names, but not his taxonomy.

DUI—Description under the influence

We devoted several postpublication discussions to reconsidering whether Linnaeus could have had Am-min in mind since his first sketch of it in 1732. As mentioned, the description of the undated encounter in Flora Lapponica (Linnaeus 1737), with its long stipe and translucent pileus, not in keeping with a solid funnel shape, differs from Am-min. The cap of the common funnel-shaped Am-min with arcuate gills is usually umbilicate, so that the stem does not rise to the very top of the uplifted cap; even if it were solid, with decurrent gills, the distance from the top of the pileus to the base of the stem only approaches two cap diameters at best, significantly shy of "long" as a dependable differentiating interspecific character. This would only leave the Kalmar sighting

for consideration. Linnaeus did not state that it had a long stipe. Unmentioned characters are not proof of their absence, but in a freestanding description—even one limited to ten words or less—omission of a character increases the likelihood of its absence. However, if its author places such a description in synonymy with a species with a long stipe, especially if it is alongside several other citations that all describe or illustrate long stipes, the likelihood changes to favour that the unspecified stipe is also long. Citing the Kalmar specimen in synonymy with several long-stemmed species three different times makes this likelihood so overwhelming that interpreting it as a short-stemmed species in this situation seems overly fanciful.

While a long stem makes the Kalmar specimen similar to *A. umbellifer*, similarity is not the same as conspecificity; available evidence suggests the opposite. The Kalmar specimen had darkening gill edges and was observed on May 31. Most species of sect. *Epiphylli* do not seem to develop darker gill edges, and contrary to what we believed at the time of our original report, most species of sect. *Epiphylli* do not fruit in the spring. However, whether the Kalmar sighting was *Marasmiellus tricolor* (Alb. & Schwein.) Singer, *Mycena acicula*, Am-min, or some other similar or dissimilar vernal species, is moot. We know that descriptions of the time are likely to include elements from more than one species. Fitting a name to a protologue considers the protologue description, very clear and distinct in this case, not speculation of what the author—or anybody else—may or may not have thought before or after writing the protologue.

The most transcendent "explanation" that cropped up during our deliberations was that Linnaeus changed his descriptions as a result of falling under the influence of Micheli! Linnaeus never met Micheli. The 29-year-old Linnaeus sent a courteous letter to Micheli (Jarvis 2016), twice his age at the time. The admiring tone of his letter and the fact that it was written in the same year that Linnaeus visited Dillenius, suggests that the young man was trying to make contact with leading senior workers—a natural attempt to learn from the more experienced. Linnaeus's letter went unanswered, likely because reportedly Micheli contracted pleurisy after a collecting trip that same year, which led to his premature death. Linnaeus's entire contact with Micheli was reading Micheli's 1729 Nova plantarum genera. It is certainly an engaging book by an admirable naturalist, but to postulate that this book alone "influenced" one of the most creative minds in the field of natural history to alter his descriptions (writing "long stem" to mean short, "umbrella-like" to mean funnel-shaped, and "epiphyllic" to mean turficolous) requires covetously fervent faith. Such claim still would not explain, as Redhead & Kuyper observed, why Linnaeus did not choose to cite Micheli's Am-min-like illustrations, rather than the long-stemmed epiphyllic ones. Without explicit evidence that Linnaeus was under some bizarre otherworldly duress, we take the protologue description at face value as written, do not fantasize about influence, hidden motives, or secret codes, and merely seek a species that fits the protologue, as written, without conflict.

Luck

Completion of this quest was only made possible by unprecedented good fortune. Our luck began with the discovery that Redhead & Kuyper (1987) had already documented the major conflicts arising from trying to apply *A. umbellifer* to Am-min. Our first anticipated impediment to developing a species concept was the nature of early species descriptions: often very brief, somewhat vague, lacking important information, inconsistent, and, of course, often based on several species. Fortunately Linnaeus surprised us with a consistent cluster of solid characters that formed a very clear picture of the species he had in mind for *A. umbellifer*, making comparison for fit to a known species much easier. The hubris of requiring that we find an unequivocally concinnous fit for *A. umbellifer* was not lost on us, and we retained healthy skepticism about our ability to meet it. We set this condition knowingly at the outset, concluding from Redhead & Kuyper's experience that rejecting a name in use over 250 years may encounter some resistance, unless a convincing fit could be found to retain it elsewhere. Success would require some familiarity with Lapland mycota, something not possible from a desk, bookshelf, or armchair. This step was realized, against our own expectations, because once a clear vision of Linnaeus's concept appeared, the senior author (AV) immediately recalled a similar species he had encountered in Lapland 14 years earlier. This find was not the result of foresight, planning, or clever experimental design, but mere fortuitous happenstance. Because for several years one of his sons lived in Norwegian Lapland, AV had made multiple visits to the area, exploring the region between Finnsnes and Nordkapp, east to nearby Finland. In addition to the iconic Am-min, documented by both Rudbeck and Linnaeus, he encountered several species typical of the habitat, some of which have been reported elsewhere [*Gomphidius roseus* (Fr.) Oudem. (Aime & Voitk 2014); *Cantharellus cibarius* Fr. (Thorn & al. 2017); *Chromosera lilacina* (P. Karst.) Vizzini & Ercole (Voitk & Voitk 2020); *Arrhenia philonotis* (Lasch) Redhead & al. (Voitk & al. 2022)].

Encountering *O. umbellifera* (Figs 4, 7) in 2006 made it clear why it is not collected more frequently. For over a week AV had taken the same forest path daily to explore the barren higher land around the tree line, without seeing this species. One morning, after the first night frost, large numbers became evident on fallen leaves along the forest trail. The following day, when the photo for Fig. 4A was taken, much fewer were left, and on the third day only a few stragglers marked their passing. Scopoli (1772) confirmed that this is not a chance observation, noting "brevis vita" as one of characters of *A. umbellifer*. In other words, even if the species is common and ubiquitous, it can easily escape detection because of its unison fruiting within a very narrow timespan, and its capriciously ephemeral basidiomata. Evidently luck—covertly, at the time—was still hounding AV's steps, to guide them to that trail on those three days. Finding an epiphyllic species on fallen leaves of *P. tremula*, appropriately another Linnaeus species, around 70°N may seem unexpected, but luckily Lapland is warmed by

the tail end of the Gulf Stream (Voitk 2021), enabling substantial coniferous and deciduous forests to thrive north of the Arctic Circle. As glaciation receded, the psychrophilic *P. tremula* passed through Fennoscandia and the Baltic Sea islands to traverse Lapland, and reach the Kola Peninsula and beyond. We suspect that with it came *O. umbellifera*, a species our sequencing showed to be common in Lapland, that accommodates Linnaeus's protologue for *A. umbellifer* better than any earlier attempt, served up to us by serendipity on the aspen-lined Lapland trail (Fig. 4).

The feeling that we stumbled on a discovery—no matter how small and insignificant in a wider context, no matter whether by luck or design—that had eluded mycologists for some two centuries, is extremely gratifying. The purpose of this report is to share a disposition of names, which fits the original material without conflict, reflects their authors' intent, and observes current rules of nomenclature. While we prefer this solution, we recognize that centuries of conflict-producing names may have endeared penally catachrestic misapplications to some users, so that enthusiasm for yet another change of new old names, no matter how apt, may be reluctant. To us, this unique copernican experience is its own reward. We do not to wish to emulate the past by launching an adversarial public debate, or to engage in further brouhaha to advocate our solution, but merely content ourselves with presenting this solution together with the new information supporting it, so that our colleagues can judge whether to accept, modify or reject it.

EPILOGUE

> The Preamble to the Code states, "The object of the rules is to put the nomenclature of the past into order and to provide for that of the future ... The only proper [reason] for changing a name [is] ... a more profound knowledge of the facts resulting from adequate taxonomic study ..." We believe our solution embodies this object, while settling a longstanding problem. The major attraction of this solution is its pleasing concinnity: this application of the epithet *umbellifer* will be the first in over two centuries that will fit the concept of its author, Linnaeus, without conflict, and the familiar *A. ericetorum* will be reinstated, hopefully to continue the stability it enjoyed earlier. Names fitting with their original material without conflict are unlikely to need change, ensuring future stability in return for minimal transient discomfort. We wish to leave stable names to our colleagues of tomorrow, rather than ask them to accept ill-fitting names because for a brief period in the long history of these names we may have become comfortably accustomed to one particular version of their misapplication.

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